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The Distribution of Cladoceran Remains in Surficial Sediments From Three Northern Indiana Lakes¹

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ABSTRACT

The chitinous exuviae of Cladocera are abundantly preserved in lacustrine sediments. These remains, most of which are identifiable to species, are distributed over an entire lake floor into definite patterns governed by the cladoceran habitats and the post-depositional movements of the remains. The two primary habitats are the littoral and planktonic zones, with the members of the family Chydoridae being the dominant littoral contributors of remains and the genera *Daphnia* and *Bosmina* being the main planktonic zone cladocerans.

The distribution of remains over the lake floor was investigated by examining surficial sediment obtained from dredge hauls taken along transects in three northern Indiana glacial lakes. Qualitatively, any sediment sample is fairly representative of any other lake floor site in a given lake from the standpoint of the littoral species present and their percentage composition. This is true even though the littoral remains decline in relative abundance with increasing depth and distance from their inshore zone of production, suggesting that the remains are well integrated before being transported offshore. An examination of a single deep-water sample from each of six northern Indiana lakes shows a direct relationship between the relative proportion of littoral and planktonic remains and the relative littoral floor area and planktonic zone volume. Thus, the changing littoral-planktonic proportion of remains found in spectra of sedimentary cores might be useful in indicating the relative dominance of littoral or planktonic production following periods of lake expansion or contraction.

The quantitative distribution was expressed as the number of remains/gram organic + residue, i.e., dry weight less calcium carbonate. Littoral remains decreased in abundance with increasing depth, with a plateau near the upper portion of the hypolimnion. Planktonic remains were at maximum abundance in the same region, with decreasing numbers towards shore and deeper water. The transitional nature of the distributions in the upper hypolimnion could not be attributed to either increased fragmentation or habitation by living Cladocera. The available evidence suggests a removal of non-cladoceran sediment constituents from this region with subsequent redeposition downslope. The removal tends to concentrate the remains, while deposition further dilutes those remains found in the lower hypolimnion.

Sediment collectors were maintained in one of the lakes during the summer and fall of three consecutive years. Littoral remains were redeposited offshore during fall overturn as well as during summer stratification due to the complete circulation of epilimnetic water over the littoral. At fall overturn, deep-water surface sediments were elevated at least 1 m into the water column as shown by a similarity between all cladoceran remain analyses in the lowermost collecting vessel and the adjacent surface sediment. This similarity further suggests that although the surface sediment is raised at least 1 m into the circulating water column, it is not laterally displaced to any detectable extent that would grossly alter the sedimentary cladoceran remain population. Because of the discreteness of the littoral and planktonic cladoceran habitats, the accumulation of these remains in collector vessels promises to be useful as an indicator of sources of lake sediment.

¹Contribution No. 748, Department of Zoology, Indiana University. Based on a dissertation for the Ph.D. degree, Department of Zoology, Indiana University, September, 1962.

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INTRODUCTION

The exoskeletal remains of Cladocera found in lake sediments are of particular interest as a tool for the interpretation of lake ontogeny, the determination of relative changes in basin morphometry, and as ecological indicators of past production. The members of the family Chydoridae are represented among the Cladocera by the greatest diversity of sedimentary remains. Although the chydorids are the dominant cladocerans of the littoral fauna, their remains also occur abundantly in offshore sediments. The planktonic zone likewise is inhabited by a cladoceran fauna that contributes remains to the sediments. The objective of this study was to determine the extent of integration in surficial sediment of cladoceran remains contributed by the littoral and planktonic communities and to determine any changes in relative composition that might be occurring among the chydorid remains as they are transported offshore, including an examination of the factors responsible for these distributions. From these results it should then be possible to decide how adequately a single

sediment analysis reflects the overall sedimentary cladoceran population of a lake, and to determine differences in composition resulting from depth or increasing distance from a zone of production.

The potentialities of cladoceran remains in interpreting lake history were shown by Frey (1958) on an extinct lake in north Germany. This was followed by a report (Frey, 1961a) on a core from Schleinsee substantiating the use of qualitative and quantitative changes in cladoceran populations as indicators of lake ontogeny. Deevey (1942) assumed that *Bosmina* remains in Lower Linsley Pond bore a positive relation to the density of the producing population, and in Pyramid Valley, New Zealand, Deevey (1955) stressed the quantitative shifts in a chydorid population dominated by one species. Brehm *et al.* (1948) estimated cladoceran species abundance and attempted to correlate the relative abundance of chydorids and planktonic species along with the abundance of rhizopods with fluctuations in lake morphometry and water levels.

All previous studies on sedimentary cladoceran remains were carried out on material obtained from only one or two cores from each lake. Conclusions were based on the assumption that a single offshore core is typical of the entire lake. This idea has never been tested, at least for Cladocera. For the interpretations of single cores as well as isolated samples from contemporary sediment to be valid, it is necessary to investigate how representative these analyses are for the entire lake. Prior to this study, the only extensive work on remains in surficial sediment was that by Frey (1960a) on a single offshore sample from each of the five lakes at Madison, Wisconsin. His results demonstrated that remains preserved in offshort sediments reflect quite closely the living population with respect to the species present. A biogeographic study of sedimentary Cladocera based on a single offshore collection from each of 45 lakes in the Mississippi Valley was performed by DeCosta (1964).

DESCRIPTION OF THE LAKES

This study was carried out on the surficial sediment of three northern Indiana glacial lakes of contrasting size. The most important factors in their selection were the relatively simple shape of their basins compared to many of those in the Indiana lake district and the abundance of cladoceran remains in the sediments. Furthermore, it was desired that *Bosmina* not dominate the population, since the termination of counting depends upon the recovery of a certain number of chydorids, and a great excess of *Bosmina* over the chydorids extends the counting process. After a preliminary analysis of a single offshore sample from seven lakes, the following three were selected.

Winona Lake

Winona Lake is located in Sec. 15, 16, 21, and 22, T 32 N, R 6 E of Kosciusko County, Indiana, near the city of Warsaw. It is a kettle-hole type of glacial basin located on the western border of the Packerton moraine. Three streams—Cherry Creek, Sugar Creek, and an unnamed stream at the southeast—enter the lake. The outlet is via Little Eagle

Lake, a 20.8 ha bay at the northwest corner. Little Eagle was not considered in this study, and is not included in the morphometric data for Winona presented in Table 1.

Two conspicuous features interrupt the otherwise rather uniform slopes of the Winona basin. These are the marl knobs ("marl islands") near the south end of the lake. In studying the sedimentary deposits and

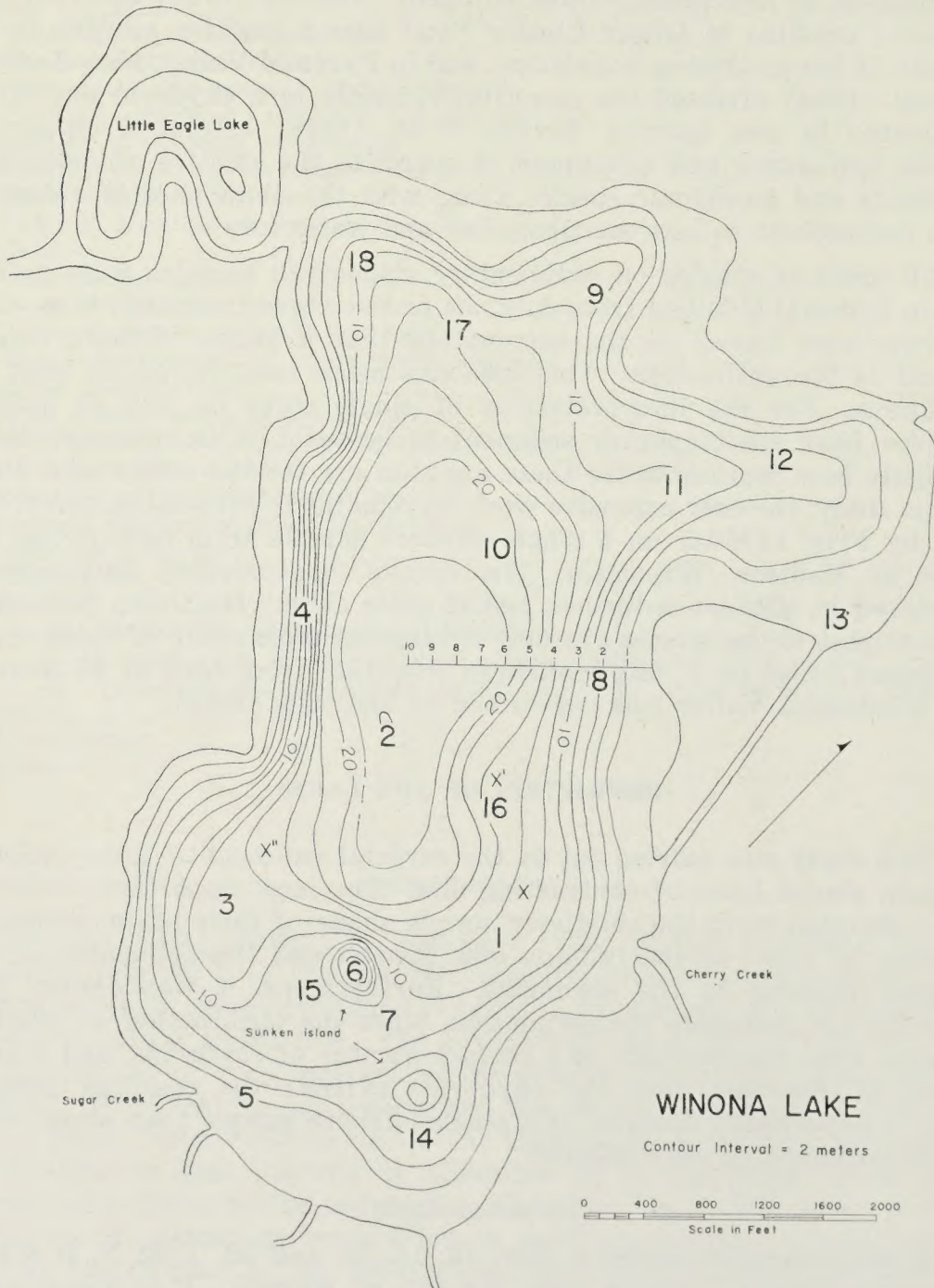


FIG. 1. Hydrographic map of Winona Lake. Sampling stations along the transect are shown in small numbers. Numbers 1 to 18 mark the non-transect sites. Sediment collector locations for 1959, 1960, and 1961 are designated X, X', and X'' respectively. (From a map prepared by Will Scott about 1935).

TABLE 1. Morphometric data and metalimnetic limits for Winona, Wyland, and Lawrence lakes. All measurements except the last were obtained by the writer from the maps in Figures 1, 2, and 3.

	Winona	Wyland	Lawrence
Area (ha)	203.7	3.43	27.4
Volume ($\text{m}^3 \times 10^6$)	18.4	0.13	1.91
Maximum depth (m)	24.4	6.3	19.2
Mean depth (m)	9.07	3.82	7.00
Mean/maximum depth	0.372	0.607	0.365
Volume development	1.12	1.82	1.09
Length of shoreline (m)	7085	857	2644
Shoreline development	1.40	1.31	1.43
Metalimnetic limits (m)	4-10	2-4	3-9

the form of the original basin of Winona, Wilson (1936) found these knobs to be accumulations of calcareous sediment on the top of knobs on the original lake bottom and not the result of subaqueous springs as suggested by Blatchley and Ashley (1900). Wilson reasoned that planation by waves of any increment of sediment prevents these knobs from reaching the surface. These local interruptions of the basin slope affect sedimentation as shown by Scott and Miner (1936) and later in this study.

Winona is a eutrophic lake with dense summer crops of bluegreen algae, which contribute to the "plankton rain" and reduce the transparency. Summer and fall secchi disc readings during the course of this study ranged from 0.6 to 2.7 m with an average of 1.2 m. These readings are considerably less than secchi disc readings made some decades earlier. For example, Juday (1902) reported that during the summer of 1901 the transparency ranged from 2.1 to 2.6 m. Henry (1914) observed a range from 2.7 to 4.0 m and stated that sufficient oxygen was present at all depths to support life; on 21 August 1912 the oxygen value at 24 m was 3.6 ppm. In contrast, the lake presently experiences a complete disappearance of hypolimnetic oxygen by mid July, indicating a marked eutrophication over the past half century. Contributing to eutrophication was a build up of the drainage basin with many homes, summer camps, and the town of Winona Lake on the east shore. The town presently dumps partially treated sewage into the lake via Cherry Creek.

The littoral vegetation of Winona is exceedingly sparse. In most areas the littoral floor is bare sand and marl. Since littoral Cladocera can be collected most readily in vegetation, such collections were taken principally from the few abundantly vegetated areas. For a short distance south of the Cherry Creek inlet *Potamogeton crispus* and *Ceratophyllum demersum* rise to the surface from a depth of 2 m. The same species are abundant at the south end of the lake where an excellent habitat was found for nearly all species of littoral Cladocera occurring in the lake. At the southeast end of the lake is a small growth of water lilies. Near the south entrance to the man-made canal are large concrete blocks densely covered with sessile algae. Surprisingly, the littoral zone of the northeast bay is completely bare, while the north shore has oc-

casional patches of rooted aquatics. The lack of vegetation today can be compared with conditions at the turn of the century, when Youse (1901) described a "luxuriant growth" and photographed areas, presently bare, that were choked with aquatics.

Further limnological data on Winona are presented in Table 2.

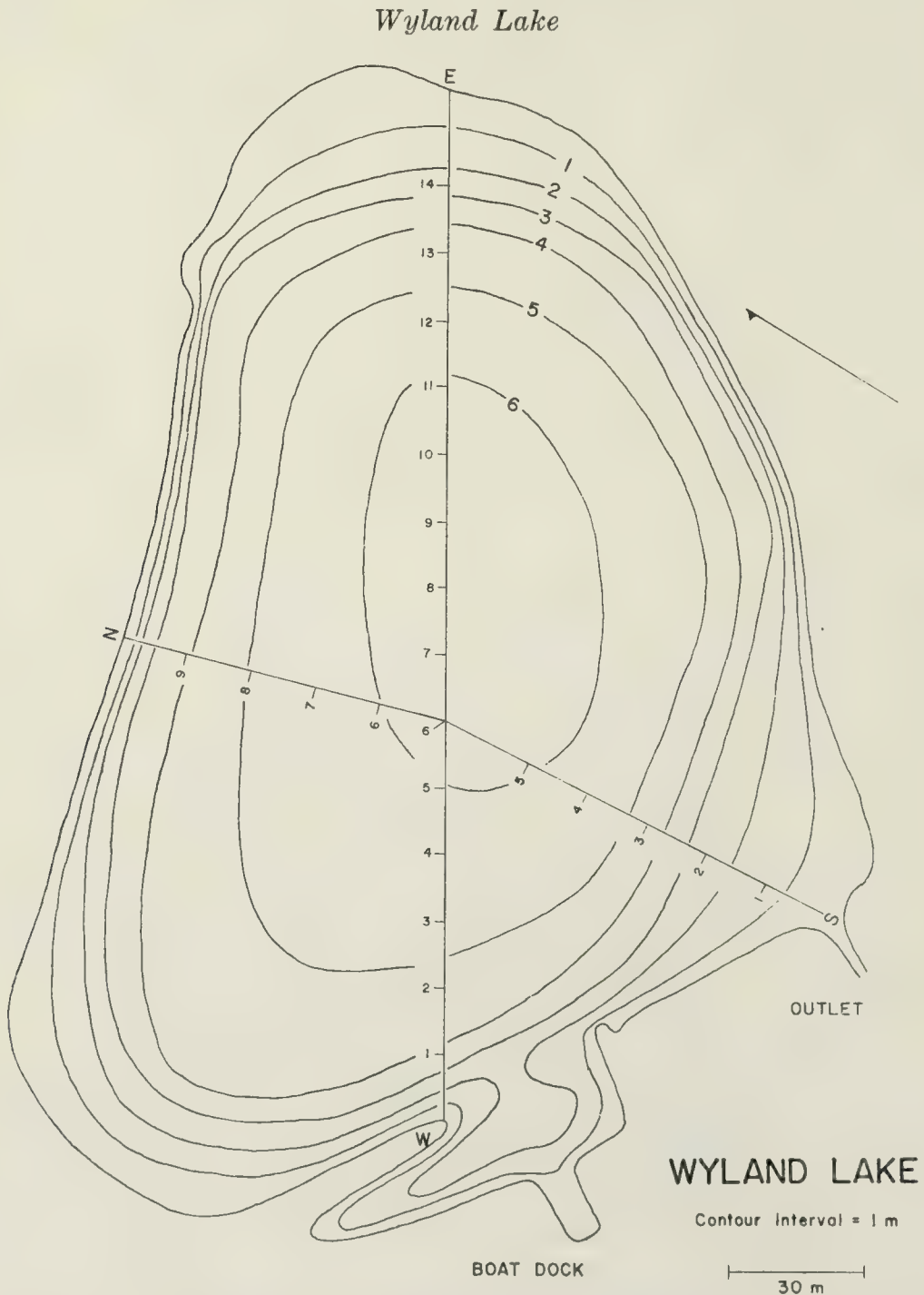


FIG. 2. Hydrographic map of Wyland Lake. Sampling stations along the west-to-east and south-to-north transects are shown. (Map prepared by D. K. Hennon and S. D. Gerking, July, 1954.)

TABLE 2. Physical and chemical data on the surface water of Winona, Wyland, and Lawrence lakes. The data from Winona and Lawrence were taken during the summer of 1961. The data from Wyland are from Gerking (1962).

	Winona	Wyland	Lawrence
pH	8.3-8.7	8.4-8.5	7.0-8.7
Acid combining capacity (m.e.)	2.52-3.34	3.01-3.16	2.0-3.6
Total dissolved solids (mg/L)	282		
Dissolved color (ppm)	40		12-16
Conductivity (micromhos)	356		
Surface temp. (°C)	23.7-27.0	25.8-30.3	24.4-29.1

Wyland is a small, privately owned eutrophic lake located four miles southeast of Winona Lake in Kosciusko County, Indiana, in NE $\frac{1}{4}$ Sec. 36, T 32 N, R 6 E. Geologically the lake is on the Packerton moraine, and the simple saucer-shaped basin suggests an origin from morainal irregularities. Morphometric data are presented in Table 1.

Except for a small open area near the man-made lagoon west of the outlet, the lake is surrounded by a dense deciduous woodland that contributes a compact leaf litter to the adjacent drainage area. The streams entering the lake are quite small and temporary, and much water enters as unconcentrated runoff through the leaf litter. Some soil from farmland beyond the woods at the east end enters through small channels.

Because of its small size and surrounding woodland the lake is protected from wind, which, coupled with other factors, aids in the development of a metalimnetic oxygen maximum as illustrated by Eberly (1959). Gerking (1962) also observed such an oxygen maximum, which once attained 25.5 ppm at 3 m. The algae found abundantly in the metalimnion during the maximum were *Oscillatoria prolifica*, *O. agardhii*, and *O. rubescens*. The oxygen maximum disappeared by late summer, and a clinograde oxygen curve prevailed thereafter.

The most abundant submersed plant is *Chara*, which completely covers the shallow-water bottom of the lake. Beyond the *Chara* in deeper water is *Potamogeton pectinatus*. Scattered at various points along the margin are *Ceratophyllum*, *Myriophyllum*, *Nuphar*, and *Nymphaea*. Only a few patches of water lilies are found.

At the peak of the phytoplankton bloom in early summer the compensation level or lower limit of positive assimilation balance lies between 2 and 3 m, but after a decline of the phytoplankton in August this drops to 4 m. Additional limnological data are given in Table 2.

Lawrence Lake

Lawrence Lake is part of the Twin Lakes chain located about four miles southwest of Plymouth, Indiana, in Marshall County, Sec. 19, T 33 N, R 2 E. This chain is a group of six lakes, four of which are in linear sequence. Lawrence Lake heads the group, followed downstream by Myers, Cook, and Mill Pond lakes. The outlet of Lawrence feeds directly into Myers Lake through a short culvert, which maintains the surface elevation of both lakes at 769 ft. The immediate watershed area is quite small because the land slopes away from the top of a ridge closely surrounding the lake. Along the south and southeast margin temporary



FIG. 3. Hydrographic map of Lawrence Lake. Sampling stations along the north, south, and west transects are shown. (Map prepared from U.S.G.S. and Indiana Department of Conservation data.)

rivulets flow over sloping farmland. The steep ridge to the north is continuous with the north margin of Myers Lake and forms a divide between the two lakes and the Yellow River, which represents a completely different drainage system.

Lawrence Lake is on the Maxinkukee moraine, an end moraine formed at the west boundry of the Saginaw lobe of the Cary substage of the Wisconsin glacial stage. Eberly (1959) discussed the uncertain origin of the Twin Lakes chain and concluded that each of the lakes in the chain is an ice block basin except Mill Pond, which was created by a dam in Forge Creek downstream from the lake chain. Morphometric data are given in Table 1.

Frey (1955a) listed Lawrence among the Indiana Lakes with cisco populations that are fished. The "cisco layer," defined as the stratum having an oxygen content greater than 3 ppm and temperatures less than 20°C, lies between 5 m and 12.5 m. From 12.5 m to maximum depth the oxygen value is ca. 1 ppm. Since the metalimnion lies between 3 and 9 m, the cisco are confined to the lower metalimnion and upper hypolimnion. Frey once observed a plus heterograde oxygen curve in Lawrence Lake, and on 17 July 1953 Eberly (1959) found 11.3 ppm oxygen at 6 m. This same type of metalimnetic oxygen maximum occurs in adjacent

Myers Lake studied by Eberly, and since Myers is also a cisco lake, a similarity of limnological conditions of the two lakes is suggested.

Rooted vegetation is widely distributed and consists mainly of *Potamogeton* and *Myriophyllum*. Water lilies are abundant near the outlet and in the extensive shallow area to the south and east. Emergent plants in these same regions blend in with terrestrial vegetation and hide the shore line.

METHODS

Collection of Surficial Sediment

All samples of surface sediment were collected with a 225-cm² Ekman dredge that was carefully lowered into the sediment to avoid complete imbedding. The dredge was hauled to the surface, opened from the top, and no more than 2 to 3 cm of surface sediment was removed. The sediment was stored at 5°C until analyzed. Assuming a sedimentation rate of 2 to 3 mm/yr, as did Frey (1960a), the uppermost 3 cm of sediment would represent a maximum accumulation of 15 years.

The 18 non-transect samples from Winona Lake were taken from a boat. Each sampling location was determined with a fair degree of accuracy by obtaining fixes on previously established shore locations with a pelorus rod. Sampling sites were selected because of their proximity to the marl knobs, slope of the bottom, valley profile, point of maximum depth, or nature of the littoral zone sediment. These sampling locations are shown on the Winona map (Fig. 1), and the measured depth at each is presented in Table 3. Because these 18 samples were difficult to interpret in terms of the lake as a whole, subsequent sampling of Winona and all the sampling of the other two lakes was done along transects.

Transect samples were taken through ice at equally spaced locations running from shore to deep water. The location of the transects was determined with a plane table and alidade. The distance between successive transect stations and the depth at each station are given in Table 3.

Three transects were made in Lawrence Lake (Fig. 3), each beginning at 18.8 m near the point of maximum depth and progressing towards the north, west, or south shores. These approximate directions give variation in the length of the transect lines and slope of the lake bottom. The south transect was also chosen because of the extensive littoral bay near shore and the valley-like profile beyond.

Each of the two Wyland Lake transects extends from shore to shore across the central plain of the lake (Fig. 2). Sample WE-6 of the west-to-east transect lies along the south-to-north transect, and for this reason WE-6 is considered with the south-to-north transect and equally spaced along it.

A single transect was made in Winona Lake (Fig. 1). The apparent uniformity of the slope shown on the map contributed to the selection

TABLE 3. Stations and depth for each transect sample of Winona, Wyland, and Lawrence lakes, and the non-transect samples from Winona. All transect samples were taken 10 and 11 February 1961 and the non-transect samples during the summer of 1959. The measured distance between successive transect stations was 50 m in Winona, 15 m in both Wyland transects (except 21 m between Sta. SN-5 and WE-6), 20 m in Lawrence North and West transects, and 30 m in the South transect (except for 16 m between Sta. S-13 and W-11).

Winona Lake					
Non-transect Samples			Transect Samples		
Station	Depth (m)		Station		Depth (m)
SS-1	13.0		T-1		1.4
SS-2	24.0		T-2		8.0
SS-3	14.0		T-3		12.5
SS-4	9.3		T-4		13.0
SS-5	2.0		T-5		14.3
SS-6	1.5		T-6		21.5
SS-7	9.1		T-7		23.0
SS-8	6.0		T-8		23.1
SS-9	9.0		T-9		23.1
SS-10	20.5		T-10		23.3
SS-11	10.0				
SS-12	6.3				
SS-13	1.1				
SS-14	6.1				
SS-15	9.2				
SS-16	15.7				
SS-17	12.5				
SS-18	9.7				

Wyland Lake					
Station	Depth (m)		Station		Depth (m)
WE-1	2.5		SN-1		2.6
WE-2	3.7		SN-2		3.9
WE-3	4.7		SN-3		4.9
WE-4	5.2		SN-4		5.4
WE-5	5.6		SN-5		5.8
WE-6	5.9		SN-6		6.0
WE-7	6.1		SN-7		5.8
WE-8	6.3		SN-8		5.4
WE-9	6.2		SN-9		3.8
WE-10	6.0				
WE-11	5.7				
WE-12	5.1				
WE-13	5.0				
WE-14	2.9				

Lawrence Lake					
Station	Depth (m)	Station	Depth (m)	Station	Depth (m)
N-8	1.7	W-1	1.8	S-1	0.6
N-7	9.5	W-2	9.0	S-2	--
N-6	9.6	W-3	11.8	S-3	1.1
N-5	15.3	W-4	13.8	S-4	1.2
N-4	15.9	W-5	15.2	S-5	2.0
N-3	16.4	W-6	15.6	S-6	12.6
N-2	17.5	W-7	16.5	S-7	12.7
N-1	18.4	W-8	17.6	S-8	14.6
		W-9	18.1	S-9	15.6
		W-10	18.5	S-10	16.6
		W-11	18.8	S-11	16.9
				S-12	18.0
				S-13	18.8

of this transect line, but the actual depths measured at the sampling stations indicate a more irregular slope. Since the transect passes over non-transect sample SS-8 at 6.0 m, SS-8 is included as a transect member located midway between site T-1 (1.4 m) and T-2 (8.0 m).

THE SEDIMENT COLLECTORS

Sediment collectors were maintained in Winona Lake during the summer and fall of 1959, 1960, and 1961. A different collector design was used each year in hopes of making the change of collecting vessels a one-man operation, but this plan failed. Thomas (1950) and Kleerekoper (1952) designed collectors with lids, but these devices seemed too elaborate for the present investigation. Scott and Miner (1936) tested the error from sediment loss upon removing an open collector vessel and found that the loss was "not perceptible on a balance sensitive to 0.1 g."

During 1959 a collector was constructed similar to the one used by Scott and Miner (1936) in their sedimentation studies in Winona and Tippecanoe lakes, Indiana. This device (Fig. 4), utilizing a submerged float resting 0.5 m below the surface, forms a very stable platform for the attachment of the collecting vessels. The vessels were wide-mouthed glass jars having a depth of 7 to 9 cm and a mouth diameter of about 7 cm.

Certain difficulties involved in locating and lifting this collector prompted a new design in 1960. This collector (Fig. 5) consisted of a floating 55-gal drum connected by a taut cable to an anchor. A cross arm 50-cm long was U-bolted to the cable 0.6 m below the surface. A counter weight was attached to one end of the arm and to the other the collector cable that extended to 1 m above the lake floor. The collecting jars were the same as those used in 1959. Unfortunately this design proved unreliable due to twisting of the collector and anchor cables by the slow back and forth movement of the float. This twisting increased as the fall winds increased in strength. Slack that developed in the anchor cable after installation allowed this movement.

The collector designed for 1961 (Fig. 6) used a floating drum secured from both ends by ropes extending toward the anchors. The collector cable was attached beneath the drum, and access to the cable was gained by rolling the drum in the water. The collecting vessels, consisting of 1-liter polyethylene bottles with the base cut off, were similar to ones used by Ohle (unpublished) in Grosser Plöner See. Two such bottles were inverted in a carrier as shown in Figure 7. These vessels proved to be very reliable by trapping sediment in the narrow neck. Several series were run using the previously mentioned jars, but movement of the float that was transmitted to the collector cable and vessels was sufficient to cause some sediment loss from the low-sided jars.

Certain precautions were taken to guard against an inquisitive neighboring populace. The drum was filled with styrofoam chips so that it would remain afloat even if punctured. Also, a 2 m length of chain was placed between the drum and each nylon anchor rope.

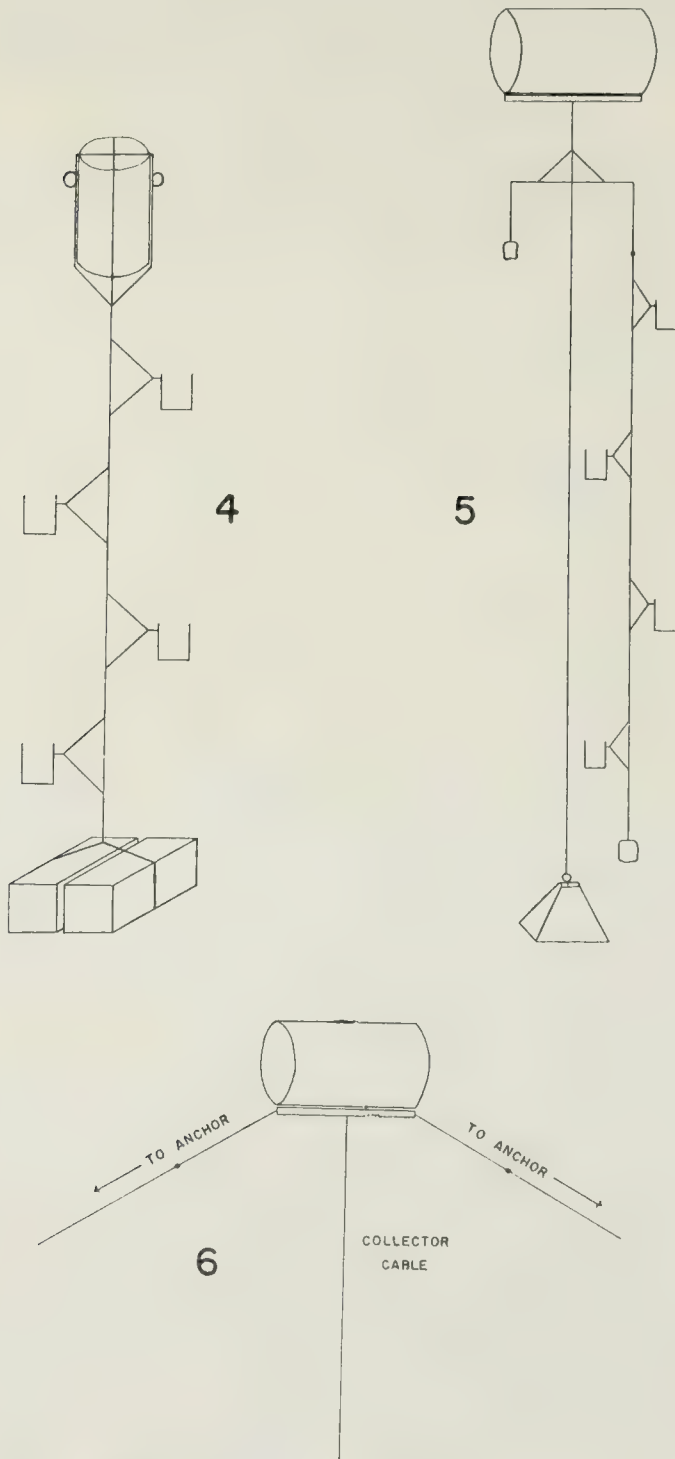


FIG. 4. Diagram of the sediment collector used in 1959.

FIG. 5. Diagram of the sediment collector used in 1960.

FIG. 6. Diagram of the sediment collector used in 1961.

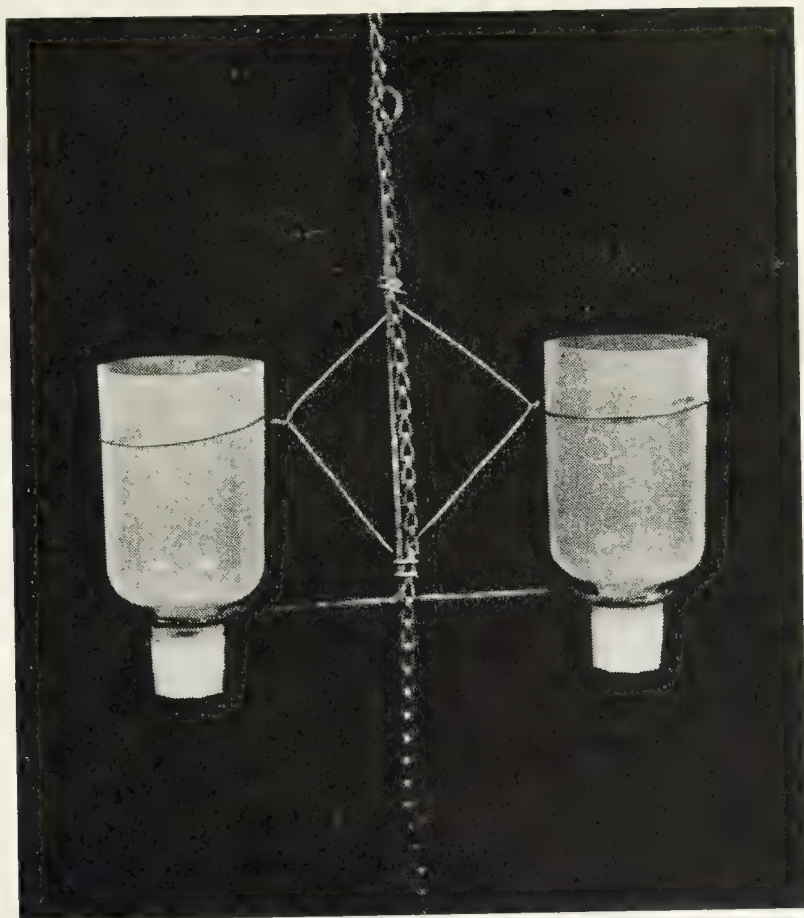


FIG. 7. Polyethylene sediment collecting vessels secured in a carrier. Four such units were attached along the collector cable shown in Figure 6.

Preparation and Analysis of the Sediment

After thorough mixing of each sample, a measured quantity of sediment was removed for the preparation of quantitative slides. When the sediments were soft and "soupy," 5 or 10 cc was removed with a 10 cc Luer glass springe. Certain littoral sediments, because of their marly nature, could not be handled in this manner and were measured in a glass tube of 6 mm internal diameter calibrated to 3.0 cc.

Each subsample of sediment was treated with 10% HCl followed by 10% KOH according to the procedure of Frey (1960a). Large quantities of silt and clay-size particles necessitated washing the treated material through a 250-mesh bronze screen. A few of the smaller cladoceran remains such as claws and fragments were lost through the screen, but nevertheless the increased visibility of the remains in screened samples actually resulted in higher counts than in non-screened samples. The remains retained by the screen, now freed of all silt and clay-size particles and carbonates, were concentrated by centrifugation and diluted to a volume dependent upon the density of remains in the sediment. Quantitative slides were then prepared by withdrawing 0.05 ml subsamples, evaporating the excess water, and mounting in glycerin jelly stained with gentian violet for differentiation of the remains. The slides were scanned at 100 x, and for each remain encountered the species and type of skeletal component was

tabulated. Each remain was also categorized as either complete or fragmented. Counting continued until at least 200 recognizable chydorid remains had been recovered.

Qualitative slides were prepared only for the non-transect samples from Winona Lake. Small portions of material remaining after preparing quantitative slides were carefully examined at 45 x under a stereoscopic microscope. The individual skeletal fragments were picked out with a whisker and mounted in polyvinyl lactophenol stained with lignin pink. For the other two lakes, the species list is based solely on the quantitative examination.

In preparing the material from the sediment collectors, the contents of a collector vessel were allowed to settle for 30 hr in a graduated cylinder following the recommendation of Tutin (1955). When two vessels were located at the same depth in a series, the sediments of both were combined after reading the individual volumes. Before further treatment, the sediment was examined for intact littoral Cladocera that might have been living in the vessels at the time of removal from the lake. If sufficient sediment was available, it was divided into two aliquots, one of which was used to obtain the proximate chemical composition of the sediment, and the other was prepared for quantitative analysis of the cladoceran remains using the same procedures described for the surface sediment. By calculating the area of the opening of a collector vessel, the depth of sediment/unit time and number of remains sedimented/cm²/unit time was determinable. When insufficient sediment was present for a complete analysis, the chemical determinations were omitted. Under certain circumstances only a percentage composition count of the remains could be made.

Proximate Chemical Analysis of Sediment

Measured volumes of sediment for the chemical analyses were placed in tared crucibles and dried at 95°C for 24 hr to obtain the dry weight. Each sample was then ashed at 525°C for 1 hr in a muffle furnace, and the loss of weight was considered approximately equivalent to the organic matter present. An additional weight loss obtained by ashing at 925°C for 2½ hr was considered to be due entirely to the loss of carbon dioxide from the calcium and magnesium carbonate plus some water of hydration of clay minerals. The weight of CaCO₃ equivalent was obtained by multiplying the CO₂ weight by 2.273. Subtracting this calculated CaCO₃ value from the total inorganic weight at 525°C gives the weight of non-calcareous ash or residue. This residue consisted primarily of SiO₂ in the Madison, Wisconsin lakes (Frey, 1960a). Wilson and Opdyke (1941) using a different method recorded all non-calcareous ash as "silica," but an actual determination showed a low percentage of non-siliceous residue.

Frey (1960a) considered this second ashing for determining carbonate to be reliable when the clay mineral content is low, thus minimizing the weight loss from water of hydration of clay minerals. Murray (1956) determined CaCO₃ equivalent by treating the sediment with HCl and back titrating with NaOH. A comparison of the two methods (Table 4) shows close correspondence in results when carbonate content

TABLE 4. Chemical analyses by percentage of pairs of duplicate sediment samples from Winona Lake, Indiana, and Page's Lake, North Carolina, by the methods of Murray (1956) and Frey (1960a).

	Station	Depth m	Murray's Method			Frey's Method		
			Organic*	CaCO ₃	Residue	Organic	CaCO ₃	Residue
Winona Lake	SS-6	1.5	3.6	90.6	3.8	3.6	91.4	5.0
	SS-9	9.0	12.6	59.7	27.7	12.5	60.4	27.1
	SS-11	10.0	12.1	50.0	37.9	12.2	51.2	36.6
	SS-3	14.0	12.3	33.8	53.9	12.2	35.0	52.8
	SS-2	24.0	11.2	30.1	58.7	11.3	31.5	57.2
Page's Lake		1.0	18.4	0.0	81.6	16.2	2.4	80.4
		1.7	20.5	0.0	79.5	22.1	4.4	73.5
		2.0	17.0	0.0	83.0	16.4	3.9	79.7

* All organic determinations in table by loss on ignition at 525°C, rather than by Murray's method of oxidation with chromic acid and back titration with ferrous ammonium sulfate.

is high, as it is in the Wisconsin lakes studied by Frey and by Murray as well as in the northern Indiana lakes investigated here. When Murray's method detected no CaCO₃ equivalent in several sediment samples from Page's Lake, North Carolina, Frey's method indicated from 2.4 to 4.4% CaCO₃, probably due to loss of water of hydration of clay minerals. Hence, when CaCO₃ content is quite low or absent, or when the clay content is high, Murray's method is to be preferred.

DISTRIBUTION OF CHEMICAL CONSTITUENTS

Since the quantities of cladoceran remains will be related to various chemical parameters of the surficial sediment, it is necessary to examine the percentage composition of these parameters as functions of water depth and distance from shore. The parameters used are calcium carbonate (calculated from loss on ignition between 525°C and 925°C), organic content, and residue (non-calcareous ash).

The distribution of CaCO₃ equivalent, expressed as a percentage of the total dry weight of sediment, along each transect of the three lakes is presented in Fig. 8. With the exception of the south transect in Lawrence Lake, CaCO₃ forms a high proportion of the shoreward surface sediment. As depth increases there is a rapid decline in the percentage, which shows the increasing influence of CO₂ in effecting resolution of carbonates. In the hypolimnion, the percentage stabilizes and remains fairly uniform to the deep end of the transect. The low carbonate values near shore in Lawrence's south transect are attributed to the rooted aquatics in the bay, consisting of a heavy mat of green *Myriophyllum* and decaying vegetation, which was present in such abundance that a dredge haul could not be taken at Station S-2. Thus, any accumulation of carbonates in this area would be diluted by organic matter, and of course, it is possible that the quantity of carbonates was being diminished by acids derived from organic decomposition.

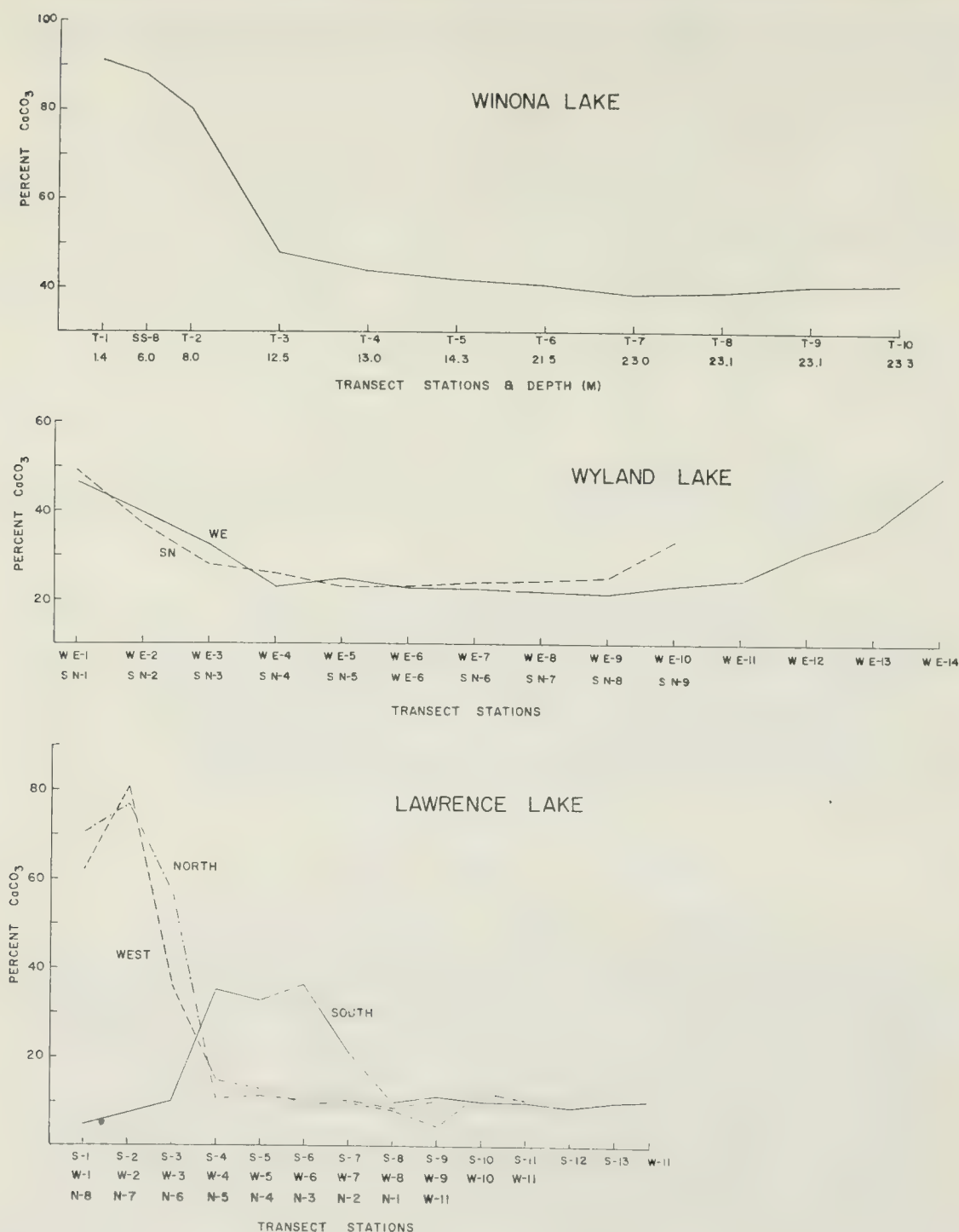


FIG. 8. Distribution of CaCO_3 equivalent along each transect from Winona, Wyland, and Lawrence lakes. The inshore stations are at the left and the offshore stations at the right of the curves. In Wyland the transects extend from shore to shore.

The organic percentages presented in Figure 9 were calculated on the basis of just two sedimentary components—organic matter and residue. By eliminating carbonates, the organic and residue values of these hard-water lakes can be compared directly with non-calcareous sediments. This eliminates the wide differences in carbonate content resulting from

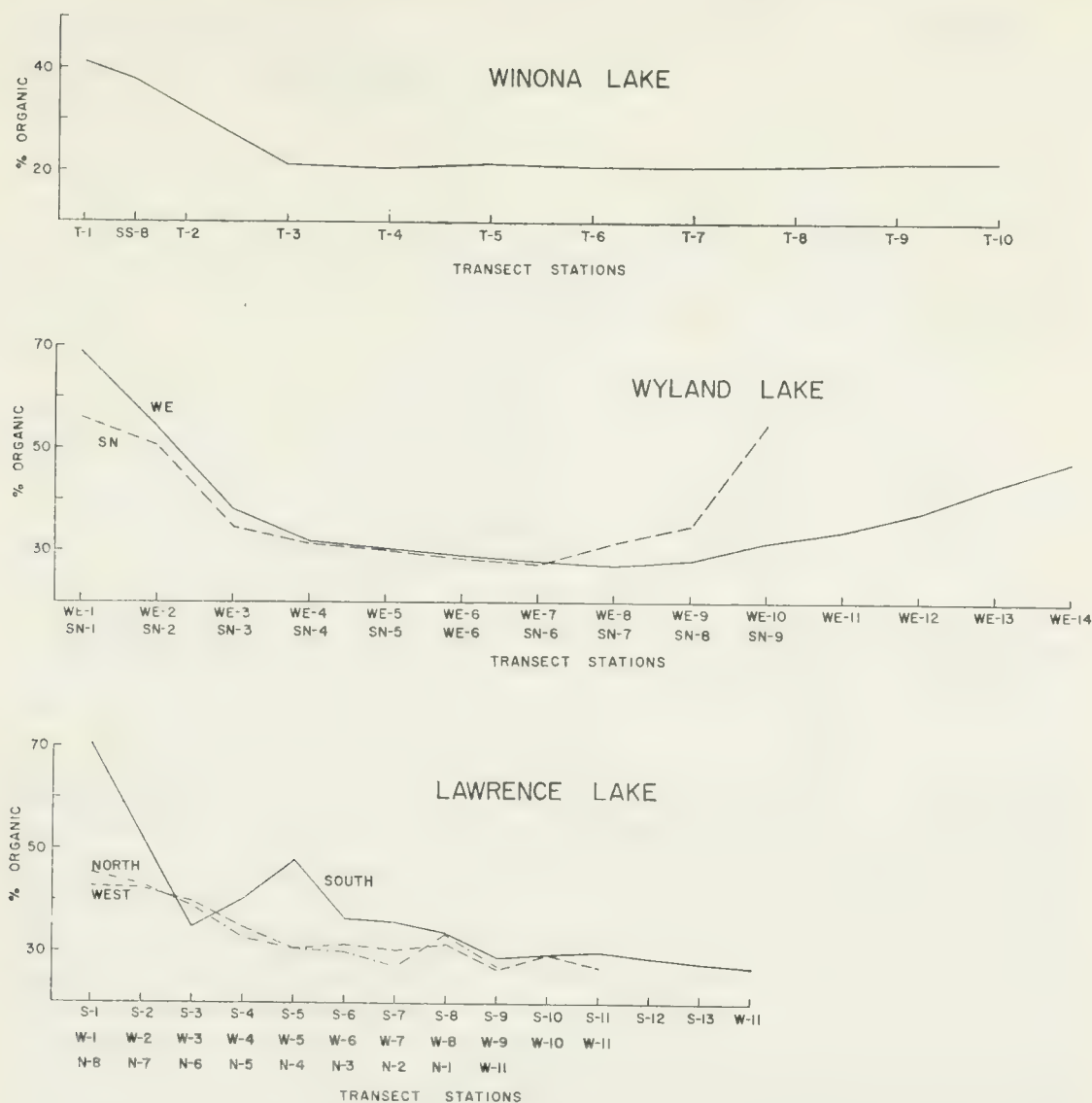


FIG. 9. Distribution of organic content along each transect from Winona, Wyland, and Lawrence lakes. The inshore stations are at the left and the offshore stations at the right of the curves. In Wyland the transects extend from shore to shore.

its variable resolution in the presence of CO_2 , especially in the hypolimnion. If carbonates were included, the variation in organic content would otherwise be dependent upon the varying degrees of calcareous resolution that occurs between inshore and offshore sediments. In each transect the highest values of organic content are near shore, and conversely this is the region of lowest residue, since only these two components are being considered. The rooted aquatics with their attached flora and fauna (Aufwuchs) are the major contributors of shallow-water organic material. Depending upon the nature of the immediate watershed, there could be some allochthonous organic additions. The high organic value of 70% in the south bay of Lawrence Lake is similar to that at the west end of Wyland. When considered on the basis of *total dry weight*, however, the value in Wyland becomes 37% and that of Lawrence remains approximately the same due to the low proportion of carbonate.

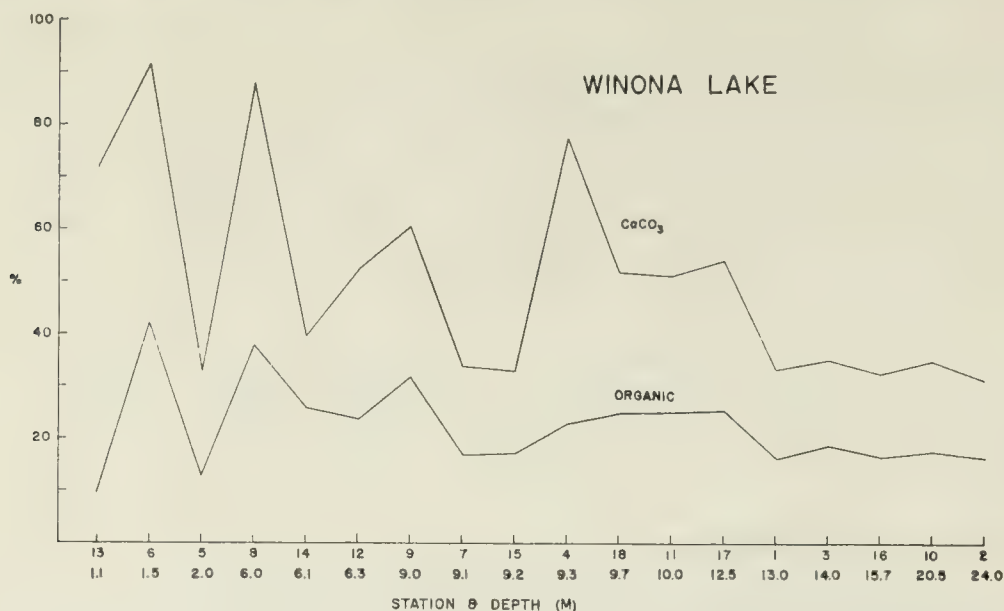


FIG. 10. Percentage of CaCO_3 equivalent and organic content for the non-transect samples from Winona Lake, arranged in order of increasing depth.

The higher residue values at the east end of Wyland are attributed to the inwash of soil from farmland lying just beyond the woodland cover on this shore of the lake. These exceptions in Lawrence and Wyland will later be used in explaining the number of cladoceran remains in these shoreward regions.

One might expect that the non-transect samples from Winona when arranged in order of increasing depth would exhibit similar progressive changes in percent chemical composition, and indeed this is true to some extent (Fig. 10). However, distance from the nearest littoral area, basin slope, and particularly proximity to the marl islands tends to distort the expected relationships. This is especially true in the CaCO_3 curve for samples SS-5, -7, -15, and -4.

SS-7 and SS-15 are located adjacent to the west marl knob (Fig. 1) that Scott and Miner (1936) found to be influencing nearby sedimentation in collector vessels. SS-5 is adjacent to a channel dredged into the south shore. The clay from this operation produces a high residue percentage and a correspondingly low carbonate value. SS-4 is on a 17% slope measured between the 2 m and 18 m contour lines, which is the steepest slope in Winona. The sediment is coarse textured, being composed of intact and finely divided mollusc shells in a marl matrix. The slope angle is probably determined by the accumulated marl and is at, or approaching, the angle of repose. Silt and clay particles slide down the face of the deposit or else are easily dislodged by currents. The original basin slope beneath this area is 14% (Wilson, 1936). This similarity of slope angles supports the idea that an angle of repose is involved.

In all three lakes, with the exceptions noted, there is a similarity in the distributional pattern of sediment constituents, although the proportions may vary. A comparison of the deep-water stations in Lawrence and also in Wyland shows a uniformity of constituents regardless of the

sediment location. Certainly, the protected setting and saucer-shaped basin of Wyland contributes to the symmetry of the curves for that lake.

IDENTIFICATION OF CLADOCERAN REMAINS AND OTHER MICROFOSSILS

Cladoceran exuviae preserved in lake sediments are generally disarticulated into their several components and occur primarily as head shields, shells, postabdomens, claws, and ephippia. Frequently the larger remains undergo further fragmentation, but usually these fragments are identifiable to species or at least genus.

The chitinous remains of the various cladoceran families do not preserve equally well after deposition, but Frey (1960a) believed that all species of chydorids and lesser numbers of the other families are represented by remains in the sediment. Certainly, the greatest species diversity is found among the chydorids. The differential preservation of the various instars has not been studied, but there is some suggestion that the later instars are selectively preserved.

In no species were the skeletal components found in a 1:1 ratio. Frey (1958) discussed the difficulty of recovering the 1:1 ratio present in the original population. Such a ratio has been approached only in *Bosmina*. Deevey (1942) found approximately equal numbers of *Bosmina* shells and head shields and hence used only one of these components in studying the quantitative fluctuations. In Wyland Lake the *Bosmina* head shield/bivalve shell ratio is 1:1.14. However, the use of a procedure similar to Deevey's would be unsuitable in the present study, because some disposition would have to be made of single shells, fragments, and antennules. Furthermore, it was only in Wyland where *Bosmina* was abundant that a 1:1 ratio was approached.

Determination of Species

Identification of the remains was accomplished primarily by comparing them with camera lucida drawings reproduced in papers by Frey (1958, 1959, 1960a, 1961b) and with the illustrations by Birge (1918) and Lilljeborg (1900). Identification of many remains was verified by Dr. Frey. Other remains were identified by comparison with living specimens collected at the lakes.

Four morphologically distinct claws of *Daphnia* were found, and a comparison with the diagnoses given by Brooks (1957) left little doubt that they are assignable to *Daphnia galeata mendotae*, *D. schödleri*, *D. retrocurva*, and *D. pulex*. Moreover, these four species were the only ones found living in Winona Lake.

Species determination of *Bosmina* was made on the basis of claw characters (Austin, 1942) and the position of a lateral pore near the fornix of the head shield. Goulden and Frey (1963) have shown that this pore is reliable for distinguishing between *Bosmina longirostris* and *B. coregoni*, which are the two species most commonly recognized in North America. DeRyke (1922) found *B. coregoni* in fish stomachs from Winona Lake, but the extensive collections for living and sedimentary cladocerans taken during this study failed to confirm his record. Only *B. longirostris* was recovered.

Head shields of *Alona rectangula* and *Alona guttata* are indistinguishable on the basis of characters now known. Any *Alona* comparing favorably in size, shape, and pore arrangement with these two species was categorized as "small *Alona*."

In every sample certain remains were recognized as belonging to the family Chydoridae, but were not assignable to a particular genus or species. Such remains were categorized as "unrecognizable" due to their fragmented condition, improper positioning on the slide, or obscuration by foreign material. Since they are chydorid remains, however, they are included in the chydorid totals.

Categories such as *Pleuroxus* sp. or *Alonella* sp. are used. Remains assigned to these groups were usually fragmented and could be assigned with certainty only to genus. In all cases, it is believed that the remains so assigned belong to one of the species already listed for the lake.

Notes on Remains not Previously Reported

Noted here are sedimentary cladoceran remains not previously reported in the literature. Among the Sididae additional segments of *Sida crystallina* and *Diaphanosoma* sp. were identified. Two species of Macrothricidae (*Drepanothrix dentata* and *Ilyocryptus sordidus*) have been recovered from lake sediments (Rossolimo, 1927; Zemp, 1941). In the present study macrothricid remains of *Ophryoxus gracilis* and *Ilyocryptus* sp. were found.

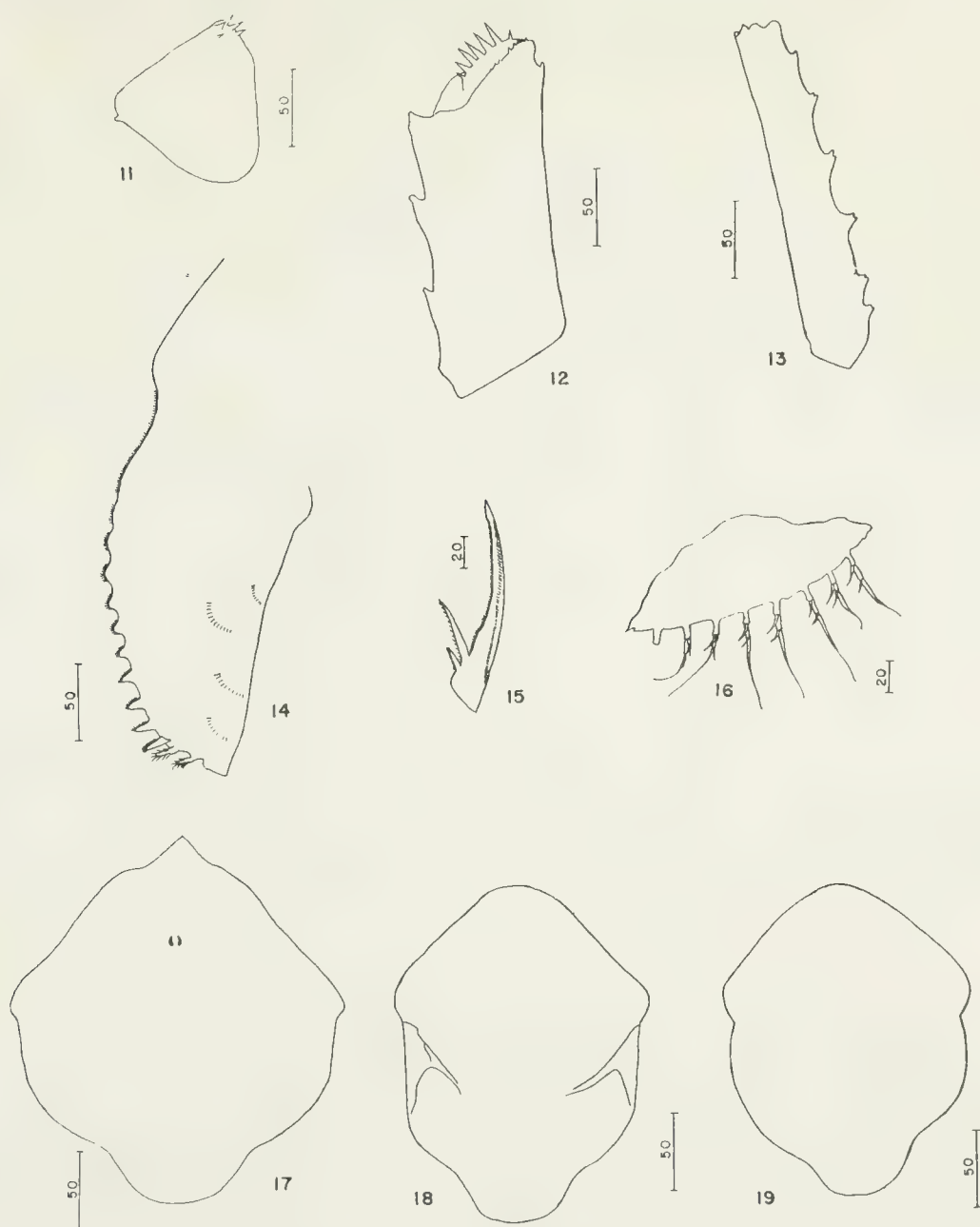
Sida crystallina. The basal exopod segment of the antenna (Fig. 11) is sub-triangular in outline with a small nipple-shaped tubercle near the dorsal basal corner. Closely spaced along the distal margin are 4 to 7 short spines. The second exopod segment (Fig. 12) is distinguished from the first (see Frey, 1960a, Plate I) by three articular tubercles of swimming hairs and a distal end oval in cross section. Part of the distal margin bears a series of minute tubercles, and opposite to these is a row of short spines, usually 7 to 9 in number.

Diaphanosoma. The terminal exopod segment of the antenna bears six marginal articular condyles of swimming hairs (Fig. 13). On the flattened distal end are two smaller condyles and a stubby spine.

Ophryoxus gracilis. The postabdomen (Fig. 14) tapers uniformly to the articular surface for the claw. The dorsal edge is provided with teeth bearing attached setae. On the more distal and pointed teeth the setae are restricted to the anterior side, but the terminal one or two teeth are digitate with bristles along the entire margin. A continuous row of setae borders the anal indentation.

The claw (Fig. 15) bears two basal spines, the distal being about three times longer than the proximal. Along the outer surface of each basal spine is a row of spinules. A row of spinules extends from the distal spine almost to the apex of the claw and also along the entire length of both lateral surfaces. Almost every claw exhibited a slight swelling before the tip.

Ilyocryptus. Only portions of the ventral shell margin (Fig. 16) with attached setae were found. The setae are quite long, and a short



- FIG. 11. *Sida crystallina*, basal exopod segment of antenna. Winona Lake.
 FIG. 12. *Sida crystallina*, second exopod segment of antenna. Lawrence Lake.
 FIG. 13. *Diaphanosoma* sp., terminal exopod segment of antenna. Winona Lake.
 FIG. 14. *Ophryoxus gracilis*, postabdomen. Lawrence Lake.
 FIG. 15. *Ophryoxus gracilis*, claw. Lawrence Lake.
 FIG. 16. *Ilyocryptus* sp., fragment of the ventral shell margin. Winona Lake.
 FIG. 17. *Alonella globulosa*, head shield. Winona Lake.
 FIG. 18. Unknown, head shield. Lawrence Lake.
 FIG. 19. Unknown, head shield. Wyland Lake.

(All figures were drawn with the aid of a camera lucida from sedimentary microfossils. The scales are in microns.)

stout spine articulates at the junctures between setal segments. Faint reticulae were occasionally seen on the shell.

Unknowns

Unidentifiable remains were only occasionally encountered. Most of these could be assigned to the family Chydoridae, but their precise identification awaits further study. Three chydorid head shields were found having no indication of major or minor pores. Frey (1958, 1959) found pores in all 43 species of chydorids he studied, and believed their arrangement has taxonomic and phylogenetic significance. Hence, the finding of a head shield lacking pores is surprising. One such head shield from Winona Lake has two chitinous thickenings shaped like parentheses near the midline (Fig. 17). Frey has identified this head shield as that of the species currently known as *Alonella globulosa*. Since all the other species of the genus *Alonella* that have been studied have a characteristic arrangement of head pores, *globulosa* very likely is improperly assigned to *Alonella*. Until this has been resolved, however, the lone head shield with the two chitinous thickenings must be designated by the present name for the species.

Head shields lacking pores as well as chitinous thickenings are shown in Figures 18 and 19. The size and shape suggest a small species of *Alona*. There is a possibility that these remains are merely aberrant head shields of common species, since in Schleinsee, for example, at certain levels a fair percentage of *Alona quadrangularis* head shields have aberrant pore patterns or even no pores (Frey, personal communication).

Other Microfossils

No attempt was made to study the distribution of non-cladoceran components in the sediments or their abundance. The most frequently encountered non-cladoceran microfossils were the head capsules of midges, which Stahl (1959) showed to be useful in unraveling lake ontogeny. Other dipteran microfossils included maces of *Glyptotendipes* and antennae and mandibles of *Chaoborus*. Among the more general insect remains were tracheal tubes, faceted portions of the compound eye, and lepidopteran wing scales.

Turbellarian egg cocoons (see Frey 1955b, 1958) were occasionally found, as well as ostracod shells, and bryozoan statoblasts. Plant remains consisted of numerous *Pediastrum* colonies and diatom frustules. *Chara* nucules were scarce.

Only Winona Lake yielded several "wheels" of the type pictured by Vallentyne and Swabey (1955) from Linsley Pond and also found in Myers Lake, Indiana by Stahl (1959). A single black sphere was found in Winona. The size of about 150μ was considerably larger than the 10 to 15μ given by Vallentyne and Swabey (1955). Upon crushing it proved to be hollow and quite brittle.

Several spines from Lawrence Lake compare favorably with the drawings by Brunson (1959) of gastrotrich spines.

CLADOCERA OCCURRING IN THE LAKES

Living Cladocera from Winona Lake

Extensive collecting in the littoral and planktonic zones was carried out during every visit to Winona in an attempt to recover species now living in the lake. Considerable effort was directed toward the littoral inhabitants, and all chydorid species except two that had previously been collected by others were recovered, plus four additional ones.

A composite list of living Cladocera from Winona is presented in Table 5. The collections by Frey (personal communication) were taken 22 September 1956. DeRyke (1922) compiled his list from Cladocera removed from fish stomachs, and although the Cladocera were not alive

TABLE 5. Living Cladocera collected from Winona Lake and the source of the record.

<i>Leptodora kindtii</i>	5, 6
<i>Sida crystallina</i>	1, 2, 4, 6
<i>Diaphanosoma leuchtenbergianum</i>	4, 5, 6
<i>Pseudosida bidentata</i>	4
<i>Daphnia galeata mendotae</i>	1, 3, 4, 5, 6
<i>Daphnia retrocurva</i>	1, 2, 3, 4, 5, 6
<i>Daphnia pulex</i>	1, 3, 4, 6
<i>Daphnia schödleri</i>	5, 6
<i>Simocephalus vetulus</i>	2, 4
<i>Simocephalus serrulatus</i>	2, 4, 6
<i>Scapholeberis kingi</i>	4, 6
<i>Ceriodaphnia reticulata</i>	4, 6
<i>Ceriodaphnia lacustris</i>	4, 6
<i>Ceriodaphnia quadrangula</i>	4, 6
<i>Bosmina longirostris</i>	1, 2, 4, 6
<i>Bosmina coregoni</i>	1
<i>Ilyocryptus sordidus</i>	6
<i>Ilyocryptus spinifer</i>	6
<i>Eurycercus lamellatus</i>	2, 4, 5, 6
<i>Camptocercus rectirostris</i>	2, 6
<i>Acroperus harpae</i>	1, 2, 4, 5, 6
<i>Kurzia latissima</i>	6
<i>Graptoleberis testudinaria</i>	2, 5, 6
<i>Leydigia leydigi</i>	2, 6
<i>Alona guttata</i>	2, 6
<i>Alona affinis</i>	6
<i>Alona quadrangularis</i>	4, 6
<i>Alona costata</i>	4
<i>Alona rectangularis</i>	2, 6
<i>Pleuroxus procurvus</i>	2, 3, 4, 5, 6
<i>Pleuroxus striatus</i>	1
<i>Pleuroxus denticulatus</i>	1, 2, 4, 5, 6
<i>Anchistropus minor</i>	6
<i>Chydorus globosus</i>	2, 6
<i>Chydorus sphaericus</i>	1, 2, 6
<i>Alonella excisa</i>	6

- 1 DeRyke (1922)
- 2 Frey (personal communication)
- 3 Henry (1914)
- 4 House (1911)
- 5 Juday (1902)
- 6 This study

they were intact and in most cases identifiable to species. The sole records of *Pleuroxus striatus* and of *Bosmina coregoni* are from fish stomachs, but the latter record is questioned.

Of the 18 species of intact chydorids collected from the lake, all were recognized in the sediments by their disarticulated remains. In addition 10 species were recovered from sediment that had not previously been recorded as living in the lake. This again attests to the ease of assembling a reasonably complete list of chydorids from their remains in lake sediments, as Frey (1960a, 1960b) first showed for the Madison lakes.

All 18 species of living chydorids recorded for Winona were represented only in sample SS-10 at 20.5 m, where 25 chydorid species were found.

Species Represented by Sedimentary Remains

A species list of Cladocera was compiled for each of the three lakes from all sediment samples analyzed. The Winona list was prepared from quantitative slides with additions from qualitative preparations. The lists for Lawrence and Wyland are based only on quantitative slides. Of a total of 41 species found in the three lakes, 29 were members of the family Chydoridae (Table 6).

The number of remains included in this study is considerable. For Winona more than 36,000 individual cladoceran remains were tabulated on quantitative slides, and several thousand more were picked over in preparing qualitative slides. Approximately 15,000 individual remains were observed in each of the other two lakes.

The number of species from Winona is the highest yet recorded from the sediments of any lake. A partial explanation may be that in the present study, surface sediment from 28 different locations was analyzed, whereas species lists in previous studies have been compiled from the examination of a single surface sample or a single spectrum in a core. The only published study that approaches the Winona totals is that of Frey (1960a) on the Madison lakes. One sample was examined from each lake and a total of 29 chydorids was recovered from 4537 remains examined. The maximum number of chydorid species found by Frey was 23 in the Lake Wingra sediment. The maximum number in this study was 25 from sample SS-10 at 20.5 m in Winona. The completeness of Frey's list is supported by comparing it with Birge's list of living Cladocera from the same lake. Frey recovered all 23 chydorid species listed by Birge except one, plus six not listed. This confirmation of completeness for the sedimentary chydorid species list from the Madison lakes can be carried over to the lakes studied here by an even more extensive sampling. With such assurance there can be little doubt that there was a reasonably complete recovery of the sedimentary chydorid population.

Sufficient effort was expended to recover many of the less abundant species, as shown by the finding of a single remain each of *Alonella globulosa* and *Chydorus piger* and only three remains of *Alona karua*.

The greater number of species in Winona than in the two smaller lakes suggests that the diversity of ecological niches for Cladocera is greater in Winona, and that the opportunity for more niches may derive from its larger size. Certainly, this is only a superficial correlation that

TABLE 6. Cladocera recovered from the surface sediment of Winona, Lawrence, and Wyland lakes.

	Winona	Lawrence	Wyland
<i>Leptodora kindtii</i>	x	x	
<i>Sida crystallina</i>	x	x	x
<i>Latona setifera</i>	x	x	x
<i>Diaphanosoma</i> sp.	x		
<i>Daphnia galeata mendotae</i>	x	x	x
<i>Daphnia retrocurva</i>	x	x	x
<i>Daphnia pulex</i>	x		
<i>Daphnia schödleri</i>	x	x	x
<i>Ceriodaphnia</i> sp.	x	x	x
<i>Bosmina longirostris</i>	x	x	x
<i>Ophryoxus gracilis</i>		x	x
<i>Ilyocryptus</i> sp.	x		
<i>Eurycercus lamellatus</i>	x	x	x
<i>Monospilus dispar</i>	x		
<i>Camptocercus rectirostris</i>	x	x	x
<i>Acroperus harpae</i>	x	x	x
<i>Kurzia latissima</i>	x	x	x
<i>Graptoleberis testudinaria</i>	x	x	x
<i>Oxyurella tenuicaudis</i>	x		x
<i>Leydigia leydigi</i>	x	x	x
<i>Alona karua</i>		x	
<i>Alona guttata</i>	x	x	x
<i>Alona affinis</i>	x	x	x
<i>Alona quadrangularis</i>	x	x	x
<i>Alona costata</i>	x	x	x
<i>Alona rectangula</i>	x	x	x
<i>Dunhevedia crassa</i>	x		
<i>Pleuroxus procurvus</i>	x	x	x
<i>Pleuroxus striatus</i>	x		x
<i>Pleuroxus denticulatus</i>	x	x	x
<i>Pleuroxus trigonellus</i>	x	x	x
<i>Anchistropus minor</i>	x	x	x
<i>Chydorus globosus</i>	x	x	x
<i>Chydorus faviformis</i>	x	x	x
<i>Chydorus sphaericus</i>	x	x	x
<i>Chydorus piger</i>	x		
<i>Alonella nana</i>	x	x	x
<i>Alonella excisa</i>	x	x	x
<i>Alonella exigua</i>	x	x	x
<i>Alonella rostrata</i>	x		x
<i>Alonella globulosa</i>	x		
Total species	39	31	32
Species of chydorids	28	22	24
Total remains identified ($\times 10^3$)	36	15	15

needs more investigation from the standpoint of cladoceran ecology—an almost untouched area of investigation.

ECOLOGICAL CONSIDERATIONS

Among the Cladocera the substrate species are primarily restricted to the littoral zone. If these organisms dwell on or in the sublittoral or profundal sediment, it is conceivable that the addition of remains molted

in situ might accumulate, yet the interpretation would be that such remains arrived at these deeper locations through redeposition of exuviae produced in littoral areas. It is necessary then to consider the presence and abundance of substate Cladocera living beyond the littoral.

Bigelow (1928) listed the Cladocera found in the ooze film and associated ooze film assemblages. These ecological groupings consisted of littoral benthic microorganisms. Most of the associated ooze film inhabitants were Cladocera (13 species). Moore (1939) found 14 species of Cladocera among the bottom deposits of Douglas Lake, Michigan, but of the substrate associates only five species occurred beyond the littoral, and *Leydigia leydigi* was the only one below 11 m. Moore considered the occurrence of *Bosmina* sp. in the bottom population to be accidental. The only living cladocerans Cole (1955) found among the microbenthic fauna beyond the littoral zone were occasional *Ilyocryptus sordidus* and *Leydigia leydigi*, and a few plankters on the profundal bottom during the first few days of overturn. Hence, although some "littoral" Cladocera can be living offshore as members of the microbenthos, it appears that these would produce only a small proportion of the total remains of these species in deep-water sediment.

If substrate Cladocera were living in association with sediment, one might expect to recover complete exuviae as an indication of their presence along with the disarticulated remains. Unfortunately, even in the littoral sediments from the lakes studied here, there was an absence of intact exuviae or combinations of remains such as Frey (1958) found abundantly in Wallensen. The only exception was several complete exuviae of *Ilyocryptus* sp. at SS-13 of Winona.

The most abundantly preserved substrate Cladocera are the Chydoridae that occur primarily in the littoral. *Chydorus sphaericus* is the only chydorid commonly found as a plankter (Rylov, 1935). Frey (1960a) mentioned a positive correlation between the occurrence of *sphaericus* and bluegreen algae in the plankton of the Madison lakes based on observations by Birge, and Frey presented data showing tremendous numbers of *sphaericus* in the plankton. The assignment of *C. sphaericus* to a strictly littoral or planktonic habitat, therefore, cannot always be made with certainty. Obviously our understanding of its ecology is incomplete. Perhaps we are not dealing with a single species, or possibly the observed habitat differences are due to responses of varieties of *sphaericus* to different ecological conditions. In Winona *sphaericus* is chiefly littoral. Occasionally it was found in the plankton but never at a density greater than 1 organism/liter to a depth of 4 m.

Both *Daphnia* and *Bosmina* are plankters, but they may also be represented in the weedy marginal areas. A few *Bosmina longirostris* were found in nearly all littoral collections, but the abundance was insignificant compared with that in open water. In England, W. J. P. Smyly (personal communication) finds this species as a plankter in marginal weed beds, while *B. coregoni* is an open water species.

The cladoceran remains encountered in this study have been broadly divided into those derived from littoral-zone species and those from planktonic-zone species. These two categories are useful for determining

the relative influence of the shallow-water and planktonic zones of production. Their changing proportion with increasing depth and distance from the littoral zone can be used to indicate the dynamics involved in the offshore movement of remains and also the source of accumulated sediment in collector vessels. The representatives of these two categories as used in this paper are as follows:

Littoral-zone Cladocera

Family Chydoridae
Sida crystallina
Latona setifera
Ilyocryptus
Ophryoxus

Planktonic-zone Cladocera

Leptodora kindtii
Diaphanosoma
Daphnia
Ceriodaphnia
Bosmina

It is felt that the members of these groups are sufficiently discrete and that there is relatively little exchange between the two groups. The cladocerans whose remains dominate the sedimentary population are the Chydoridae, *Daphnia*, and *Bosmina*.

VARIATION AMONG CLOSELY SPACED SAMPLES

To give some indication of the variation that might be expected within a small area of lake floor, five closely spaced samples from Lawrence Lake were analyzed. These samples were all taken through the ice at distances of 2 m to the north, south, east, and west of station W-11 at 18.8 m. The sediment was handled with great care so that any error introduced during the analysis would be minimal, and hence the observed variation can be attributed to conditions existing in the sediment. Variation is expected in any sampling, but because of the necessary manipulation an opportunity exists for introducing variation beyond that inherent in the sediment. The major problem in preparing cladoceran remains for microscopic examination is to free them from the silty calcareous matrix. A procedure that would reduce or eliminate the extensive handling described in the Methods section has not been developed.

In Table 7 the percentage composition of chydorids from the five samples are arranged in order of decreasing numerical abundance. The number of remains/g organic + residue are given in Table 8, along with percentage composition data for various cladoceran measurements, the number of species, and also the proportion of organic content and residue. Also given are the number of remains counted in each 0.05-ml subsample.

With these data some indication can be gained of the degree of variation to be expected by repeated sampling within a small area of lake bottom. Certainly, one sample from a given point of the lake floor is typical of the immediate area, and minor shifts in the sampling location would not appreciably alter the results. In addition, the various measurements presented in these two tables should enable the reader to judge the extent of random variation occurring between different stations within a lake.

TABLE 7. Percent composition of chydorids from Lawrence Lake station W-11 and from samples 2 m to the north, south, east, and west of this station.

	Total remains	Percent composition					W-11	Mean \pm S.E.	S.D.	Confidence limits	
		N	S	E	W						
<i>Chydorus sphaericus</i>	794	51.8	53.3	50.6	50.2	48.5	50.9 \pm .772	1.726	55.7	46.1	
<i>Alonella nana</i>	114	6.4	5.5	7.1	10.6	6.2	7.2 \pm .897	2.005	12.8	1.6	
<i>Acroperus harpae</i>	111	7.8	7.6	7.2	7.3	5.9	7.1 \pm .335	0.748	9.2	5.0	
Small Alona	85	7.0	3.8	5.8	4.8	5.9	5.5 \pm .542	1.212	8.9	2.1	
<i>Alonella excisa</i>	80	4.1	7.5	6.8	2.5	5.3	5.2 \pm .904	2.022	10.8	-0.4	
<i>Eurycerus lamellatus</i>	75	5.1	5.5	3.4	4.2	5.9	4.8 \pm .453	1.014	7.6	2.0	
<i>Graptoleberis testudinaria</i>	64	4.8	3.4	5.4	3.9	3.0	4.1 \pm .443	0.990	6.8	1.4	
<i>Alona affinis</i>	35	2.6	2.1	2.0	1.4	3.3	2.3 \pm .319	0.714	4.3	1.3	
<i>Pleuroxus</i> sp.	34	2.2	1.4	2.4	1.4	3.6	2.2 \pm .405	0.906	4.7	-0.3	
<i>Alona quadrangularis</i>	34	1.3	2.1	1.4	3.9	2.0	2.1 \pm .467	1.044	5.0	-0.8	
<i>Alona rectangula</i>	34	1.9	2.1	0.3	2.8	3.6	2.1 \pm .549	1.228	5.5	-1.3	
<i>Camptocercus rectirostris</i>	30	1.6	2.4	2.4	2.2	1.0	1.9 \pm .272	0.608	3.6	0.2	
<i>Kurzia latissima</i>	26	0.3	1.0	2.0	2.8	2.0	1.6 \pm .436	0.975	4.3	-1.1	
<i>Pleuroxus denticulatus</i>	13	0.6	0.7	1.0	0.3	1.6	0.8 \pm .219	0.490	2.2	-0.6	
<i>Alonella exigua</i>	10	1.6	0.7	0.3	0.3	0.3	0.6 \pm .253	0.566	2.2	-1.0	
<i>Pleuroxus trigonellus</i>	8	0.6	0.3	1.0	0.8	0.7	0.5 \pm .167	0.374	1.5	-0.5	
<i>Alona guttata</i>	5		0.3		0.6	0.3	0.3 \pm .148	0.332	1.2	-0.6	
<i>Pleuroxus procurvus</i>	3			0.3			0.2 \pm .119	0.265	0.9	-0.5	
<i>Alona costata</i>	2			0.3		0.3	0.1 \pm .077	0.173	0.6	-0.4	
<i>Leydigia leydigi</i>	1			0.3			0.1 \pm .063	0.141	0.5	-0.3	
<i>Chydorus globosus</i>	1	0.3					0.1 \pm .063	0.141	0.5	-0.3	
<i>Chydorus faviformis</i>	1					0.3	0.1 \pm .063	0.141	0.5	-0.3	
<i>Alona karua</i>	1		0.3				0.1 \pm .063	0.141	0.5	-0.3	
<i>Alona</i> sp.	1					0.3	0.1 \pm .063	0.141	0.5	-0.3	
Total species		15	16	17	15	17					
No. of remains examined	1562	313	291	295	358	305					

TABLE 8. Additional data obtained from Lawrence Lake station W-11 and from samples 2 m to the north, south, east, and west of this station.

Remains x 10 ³ /g organic + residue							
	Total	Littoral	Planktonic	<i>Bosmina</i>	<i>Chydorus sphaericus</i>	Other chydorids	
N	97.6	67.4	30.2	13.3	32.6	34.4	
S	120.4	84.8	35.5	17.5	42.4	41.2	
E	111.9	75.2	36.7	11.6	35.3	38.8	
W	107.2	70.5	36.8	21.3	34.3	35.6	
W-11	118.3	84.0	34.3	11.0	36.8	45.6	
\bar{X}	111.1	76.4	34.7	14.9	36.3	39.1	
S.E.	4.10	3.51	1.21	1.95	1.68	2.02	
S.D.	9.17	7.84	2.71	4.37	3.75	4.52	
Percent				Percent of Chydoridae			
Sediments		Cladocera		<i>Chydorus sphaericus</i>	Other chydorids		
	Organic	Residue	Littoral	Planktonic			
N	28.5	71.5	69.1	30.9	51.7	48.3	
S	32.0	68.0	70.5	29.5	53.2	46.8	
E	28.1	71.9	67.2	32.8	50.5	49.5	
W	28.8	71.2	65.7	34.3	50.3	49.7	
W-11	27.1	72.9	71.0	29.0	48.3	51.7	
\bar{X}	28.9	71.1	68.7	31.3	50.8	49.2	
S.E.	0.85	0.85	0.98	0.98	0.85	0.85	
S.D.	1.9		2.2		1.9		
Percent of Chydoridae			Percent of total remains				
	Fragmented	Non-fragmented	<i>Bosmina</i> + <i>Daphnia</i>	<i>Chydorus sphaericus</i>	Other chydorids		
N	45.0	55.0	30.5	33.4	35.2		
S	43.6	56.4	29.5	35.2	34.2		
E	40.3	59.7	32.6	31.6	34.7		
W	32.6	67.4	33.9	32.0	33.2		
W-11	38.4	61.6	28.8	31.0	38.5		
\bar{X}	40.0	60.0	31.1	32.7	35.2		
S.E.	2.19	2.19	0.94	0.76	0.89		
S.D.	4.9		2.1	1.7	2.0		
Remains counted/cover							
	1	2	3	4	\bar{X}	S.E.	S.D.
N	126	124	102	134	121.5	6.90	13.8
S	160	152	129		147.0	8.00	16.0
E	158	158	157		157.7	0.55	1.1
W	144	135	116	168	140.7	10.80	21.6
W-11	159	163	154		158.7	2.30	4.6
Number of species							
	Chydoridae			Total			
	N	15		20			
	S	16		20			
	E	17		22			
	W	15		20			
	W-11	17		22			
	\bar{X}	16.0		20.8			
	S.E.	0.58		0.49			
	S.D.	1.3		1.1			

CHYDORID SPECIES AND THEIR PERCENTAGE COMPOSITION

Although the chydorids are associated primarily with shallow-water substrate, their remains are found abundantly in offshore as well as inshore sediments. Since only relatively small numbers of remains (except perhaps for *Chydorus sphaericus*) are actually produced at the surface of deep-water sediments or in the water overlying these sediments, the bulk of the remains occurring here must have been transported from the littoral region. To enable cores to be meaningfully used in the interpretation of lake history, the distribution of Cladocera by species composition and relative and total abundance from the littoral region to the center of the lake must be known, and the factors responsible for these distributions understood.

In Tables 9, 10, and 11 the presence of chydorid species at each station along a transect in each lake is shown, with the species arranged in order of decreasing numerical abundance. The occurrence of a species at a station is indicated by a percent value. In each transect the more abundant species occur at every station with but few exceptions. The species of lesser abundance were not recovered from every station, but it is significant that their distribution is not definitely skewed either towards the shallow-water or offshore ends of the transects. Thus, the failure to recover these species at each station probably results not from their absence at a particular site but rather from their low overall frequency of occurrence. Hence, any sediment sample or spectrum in a core should yield a species list representative of that lake if sufficient effort is expended to recover those species occurring with low frequency. Neither shallow-water nor deep-water sediments have any advantage in any study to ascertain the mere occurrence of species in a given lake. Certainly, there are no increasing or decreasing trends in species number along any transect.

The percentage composition of chydorids should reveal any shifts in the proportion of remains that might be occurring as they are displaced offshore from the predominantly inshore area of production. The percentages presented in Table 9, 10, and 11 show that although the composition is not constant for a given species along a transect, the range of variation is usually quite low. Certainly, there is no indication of a gradient for any species, although some show increases and decreases that span several sampling stations. These short gradients are considered insignificant, since they are peculiar to merely a single transect. More importantly though, such gradients are not confirmed in the same transect by species whose remains are of approximately equal size. If size is influencing the transport and redeposition of remains, then larger species such as *Eurycercus*, *Alona affinis*, and *A. quadrangularis* would be distributed as a unit, and remains of smaller species as the alonellas and small alonas would do likewise. No difference in distribution is evident.

The number of remains used for describing the chydorid percentages at each station is shown in the tables. A sample was examined until at least 200 chydorids were recovered, but in most instances considerably more remains were tabulated, since counting was never terminated until a cover slip was completely scanned. In fact, in 48 of 64 transect samples the chydorid total was over 230 remains.

TABLE 9. Chydorids from the Winona transect arranged in order of decreasing abundance, showing species occurrence and percent composition.

	Station and depth (m)												Mean	S.E.	S.D.
	Total remains	T-1 1.4	SS-8 6.0	T-2 8.0	T-3 12.5	T-4 13.0	T-5 14.3	T-6 21.5	T-7 23.0	T-8 23.1	T-9 23.1	T-10 23.3			
<i>Chydorus sphaericus</i>	1284	62.5	57.3	52.3	45.4	50.4	44.6	52.6	48.4	49.5	48.7	49.9	51.1	1.549	5.138
<i>Acroperus harpae</i>	298	5.7	7.3	9.3	14.4	11.5	13.7	12.6	14.0	11.8	11.5	14.9	11.5	0.897	2.975
<i>Camptocercus rectirostris</i>	116	2.1	2.7	6.4	7.8	6.4	3.0	5.2	3.1	4.6	4.1	5.5	4.6	0.546	1.811
Small <i>Alona</i>	114	1.6	1.2	3.4	2.9	5.5	4.5	6.8	7.9	6.0	5.5	4.5	4.0	0.655	2.173
<i>Alona quadrangularis</i>	104	4.2	8.8	4.9	3.3	0.9	4.9	0.8	2.2	3.2	2.3	8.5	4.0	0.810	2.685
<i>Eurycerus lamellatus</i>	102	5.3	5.8	4.4	4.1	2.3	3.3	3.6	3.5	1.8	3.2	6.4	4.0	0.428	1.418
<i>Leydigia leydigi</i>	98	2.6	3.8	10.3	2.5	5.0	4.5	2.0	2.6	3.2	1.4	0.9	3.6	0.774	2.565
<i>Alona rectangularis</i>	76	3.1	4.6	2.0	1.2	1.8	0.8	2.8	5.2	4.6	5.1	2.3	3.0	0.481	1.594
<i>Alona affinis</i>	64	3.6	2.7	1.0	2.9	2.3	3.0	2.8	1.3	1.4	3.7	3.2	2.5	0.280	0.927
<i>Pleuroxus</i> sp.	63	1.6	0.4	1.5	5.4	1.4	3.4	2.4	2.2	3.7	5.1	0.5	2.5	0.521	1.726
<i>Graptoleberis testudinaria</i>	61	0.5	1.9	1.0	4.1	3.2	6.3	0.8	1.3	4.1	2.3		2.3	0.579	1.921
<i>Pleuroxus denticulatus</i>	46	1.6	1.5	0.5	1.6	3.7	1.1	2.8	1.3	2.3	2.3	1.4	1.8	0.268	0.889
<i>Alonella excisa</i>	37	2.6		0.5	1.6	1.8	3.4	2.0	2.2	0.9	0.5	0.5	1.5	0.321	1.063
<i>Pleuroxus procurvus</i>	16				0.8	1.8	1.1	0.8	0.9	0.5	0.5		0.6	0.165	0.548
<i>Kurzia latissima</i>	14		0.4		0.4	0.5	0.4	0.8	1.3	1.4	0.5	0.5	0.6	0.135	0.447
<i>Chydorus faviformis</i>	12	1.0	0.8	0.5			0.8	0.8		0.5	0.9		0.5	0.151	0.500
<i>Alonella nana</i>	6	0.5					0.4	0.4	0.4		0.9		0.2	0.090	0.300
<i>Chydorus globosus</i>	5	1.0	0.8	0.5		0.5	0.4					0.5	0.2	0.113	0.374
<i>Alona guttata</i>	5								0.9				0.2	0.095	0.316
<i>Alonella</i> sp.	5			0.5	0.8	0.5		0.4	0.4				0.2	0.090	0.300
<i>Anchistropus minor</i>	4				0.4				0.9		0.5		0.2	0.090	0.300
<i>Alonella exigua</i>	3	0.5						0.4			0.5		0.1	0.068	0.224
<i>Alonella rostrata</i>	3			0.5		0.5					0.5		0.1	0.074	0.245
<i>Alona costata</i>	3			0.5	0.4					0.5			0.1	0.068	0.224
<i>Pleuroxus trigonellus</i>	1						0.4						0.1	0.043	0.141
Total species		15	13	15	15	15	17	16	16	15	18	13			
No. of remains examined	2540	207	260	205	243	218	268	249	229	218	218	220			

TABLE 10. Chydorids from the west-to-east transect of Wyland Lake arranged in order of decreasing abundance showing species occurrence and percent composition.

	Station and depth (m)														
	Total remains	WE-1 2.5	WE-2 3.7	WE-3 4.7	WE-4 5.2	WE-5 5.6	WE-6 5.9	WE-7 6.1	WE-8 6.3	WE-9 6.2	WE-10 6.0	WE-11 5.7	WE-12 5.1	WE-13 5.0	WE-14 2.9
		Mean	S.E.	S.D.											
<i>Chydorus sphaericus</i>	1989	54.0	51.3	50.3	56.0	52.1	53.1	57.9	53.6	55.2	53.3	49.8	63.6	61.0	62.5
Small Alona	276	8.5	7.8	9.0	7.3	7.8	9.7	12.7	6.4	8.9	5.5	5.9	5.8	6.3	6.7
<i>Alonella excisa</i>	251	9.0	8.9	6.9	5.2	5.3	7.0	5.3	8.9	5.7	8.6	8.0	7.3	4.3	8.1
<i>Eurycerus lamellatus</i>	119	6.5	2.6	2.8	3.5	5.3	5.0	1.2	1.5	2.9	3.0	4.0	3.1	4.3	1.1
<i>Alona rectangulara</i>	108	4.5	2.2	3.7	3.5	2.5	3.5	2.5	4.4	1.8	2.6	4.6	2.3	3.1	1.4
<i>Pleuroxus</i> sp.	111	1.5	2.6	3.2	2.4	3.3	2.3	3.7	2.3	5.7	3.8	4.3	2.3	1.6	3.2
<i>Alona affinis</i>	98	2.5	3.0	1.6	2.8	3.3	1.9	2.5	3.0	3.2	3.4	3.0	1.9	3.5	2.5
<i>Acroperus harpae</i>	93	2.5	2.6	3.2	1.7	2.5	3.5	1.6	5.4	2.1	3.0	1.8	1.5	2.7	2.7
<i>Leydigia leydigi</i>	89	2.0	5.6	3.6	2.8	0.4	2.3	0.8	1.5	1.1	4.3	2.4	3.9	2.0	1.8
<i>Graptoleberis testudinaria</i>	80	1.0	1.9	2.0	2.1	4.1	2.7	2.5	1.0	2.9	3.8	2.4	1.5	1.2	1.8
<i>Camptocercus rectirostris</i>	65	1.0	2.2	2.4	3.5	1.6	2.3	2.5	1.5	1.4	1.3	1.8	1.2	2.0	0.4
<i>Kurzia latissima</i>	62	1.5	3.3	4.1	1.0	2.5	0.8	2.0	1.0	3.2	1.3	2.1	0.4	0.4	0.4
<i>Alona quadrangularis</i>	51	1.5	1.1	2.0	2.1	4.1	0.8	1.2	1.0	0.4	0.4	2.4	1.2	0.8	0.7
<i>Pleuroxus denticulatus</i>	46	0.5	0.4	1.2	1.0	1.2	0.4	1.2	0.5	2.1	1.7	2.4	0.8	1.2	2.5
<i>Chydorus faviformis</i>	40	1.0	1.1	0.4	0.7	1.2	1.9	0.4	2.5	0.4	0.4	2.4	1.2	1.6	0.7
<i>Pleuroxus trigonellus</i>	25	0.5	0.7	0.4	1.0	1.2	0.4	0.4	1.0	1.1	0.8	1.2	0.4	0.4	0.7
<i>Pleuroxus procurvus</i>	21			1.2	1.0	0.4	0.8	0.4	0.5	0.7	0.8			0.4	0.1
<i>Alona costata</i>	16	1.0	0.4	0.8	0.7	0.4		0.4	1.0		0.4	0.9		0.4	0.5
<i>Alonella exigua</i>	13		0.7			0.4	1.2	0.8	1.0	0.4	0.8		0.4	0.4	0.5
<i>Alonella nana</i>	13	0.5	0.4		0.4		0.4	0.4	0.5	0.4		0.6	0.4		0.4
<i>Alona guttata</i>	10			0.4		0.4		0.4	1.0	0.4					
<i>Chydorus globosus</i>	9														
<i>Anchistropus minor</i>	4	0.5	0.4		0.3										
<i>Oryurella tenuicaudis</i>	2		0.4												
<i>Alonella rostrata</i>	1			0.4											
<i>Pleuroxus striatus</i>	1								0.5		0.4				
<i>Alonella</i> sp.	1		0.4												
<i>Alona</i> sp.	1					0.5									
Total species	17	19	19	19	19	17	17	17	20	18	19	16	18	19	19
No. of remains examined	3595	201	269	247	288	244	258	244	203	280	235	328	259	256	283

TABLE 11. Chydorids from the west transect of Lawrence arranged in order of decreasing abundance showing species occurrence and percent composition.

	Total remains	Station and depth (m)											Mean	S.E.	S.D.
		W-1	W-2	W-3	W-4	W-5	W-6	W-7	W-8	W-9	W-10	W-11			
<i>Chydorus sphaericus</i>	1324	50.1	39.5	50.2	44.1	49.4	51.0	50.2	49.9	45.2	48.4	48.7	47.9	1.071	3.550
<i>Acroperus harpae</i>	184	6.3	6.0	6.0	9.4	6.0	8.7	5.9	2.7	10.2	6.5	5.9	6.7	0.622	2.062
Small <i>Alona</i>	178	7.7	3.2	6.9	7.7	7.3	8.7	3.3	7.8	5.1	7.8	5.9	6.5	0.567	1.881
<i>Alonella nana</i>	175	4.8	6.8	4.6	6.8	7.7	5.2	6.6	8.5	5.9	6.1	6.2	6.3	0.357	1.183
<i>Alonella excisa</i>	172	8.1	5.6	7.4	5.6	4.7	6.5	8.0	4.3	7.1	5.6	5.2	6.2	0.394	1.308
<i>Eurycerus lamellatus</i>	143	5.8	4.8	6.0	5.2	5.6	3.5	4.4	5.5	5.1	4.8	5.9	5.2	0.228	0.755
<i>Alona quadrangularis</i>	79		14.5	4.6	3.6	0.9	1.3	1.1	0.8	2.0	1.3	2.0	2.9	1.225	4.062
<i>Graptoleberis testudinaria</i>	79	3.3	2.0	0.5	2.8	3.4	1.7	4.0	3.1	3.1	3.9	2.9	2.8	0.311	1.030
<i>Alona rectangularis</i>	75	0.4	2.0	3.7	4.0	2.6	1.7	4.4	2.3	2.4	2.6	3.6	2.7	0.349	1.158
<i>Pleuroxus</i> sp.	75	2.6	3.6	1.8	1.6	3.9	0.9	1.8	3.1	3.9	2.6	3.6	2.6	0.313	1.039
<i>Alona affinis</i>	61	1.8	4.4	3.2	1.6	0.9	3.0	1.9	0.4	1.2	2.6	3.3	2.1	0.364	1.208
<i>Camptocercus rectirostris</i>	59	3.0	0.8	1.4	1.6	1.7	3.9	2.9	3.5	1.6	2.2	1.0	2.1	0.312	1.034
<i>Kurzia latissima</i>	44	1.5	1.6	0.9	2.0	2.1	0.9	0.7	2.3	1.2	2.2	2.0	1.6	0.176	0.583
<i>Pleuroxus denticulatus</i>	23	0.4			0.4	0.4	0.4	1.8	1.6	0.8	1.3	1.6	0.8	0.200	0.663
<i>Pleuroxus trigonellus</i>	17		0.8	0.9		0.4	0.9		1.2	1.6	0.4	0.7	0.6	0.160	0.529
<i>Alona</i> sp.	15	0.4	0.8	0.5	1.2	0.9	0.4			1.2	0.4	0.3	0.6	0.128	0.424
<i>Alonella exigua</i>	15	0.4		0.9	0.4		0.9	0.4	1.2	0.8	0.9	0.3	0.6	0.121	0.400
<i>Alona guttata</i>	12	1.5			0.8	0.4		1.1	0.4			0.3	0.4	0.157	0.520
<i>Alonella</i> sp.	8	0.4	0.4		0.4	1.3		0.4		0.4	0.4		0.3	0.117	0.387
<i>Chydorus faviformis</i>	7		1.2		0.4	0.4						0.3	0.3	0.113	0.374
<i>Chydorus globosus</i>	5	1.1		0.5									0.2	0.109	0.361
<i>Leydigia leydigi</i>	4		1.2						0.6				0.2	0.117	0.387
<i>Alona costata</i>	4		0.8				0.4	0.4				0.3	0.1	0.080	0.265
<i>Anchistropus minor</i>	3						0.4			0.4			0.1	0.060	0.200
<i>Pleuroxus procurvus</i>	3	0.4								0.8			0.1	0.080	0.265
<i>Alona karua</i>	3							0.4	0.8				0.1	0.080	0.265
Total species		15	15	14	16	15	15	18	17	16	14	17			
No. of remains examined	2767	271	249	217	248	233	230	273	256	254	231	305			

The most abundant chydorid from these three lakes is the cosmopolitan *Chydorus sphaericus*, which constitutes about 50% of all chydorids in most samples, the range being 38.3% to 63.7%. Three other northern Indiana lakes sampled near maximum depth yielded similar *sphaericus* percentages. The data of DeCosta (1964) confirm that this percentage is characteristic for *sphaericus* in northern Indiana, and that it decreases toward the southern United States and increases to the north. The remaining chydorids are responding to a different complex of ecological conditions in each lake as shown by variations in the relative abundance of their sedimentary remains. This is demonstrated better by referring to the rank order of species abundance presented in Table 12 where all samples from a given lake are combined. *Chydorus sphaericus*, the most abundant chydorid, is not shown. Remains assigned to groups such as *Pleuroxus* sp. and *Alonella* sp. have been distributed among the known species within their respective genera based on the abundance of these species. Likewise, "small *Alona*" remains have been distributed among the small species of *Alona* that were identified. The following seven species are among the 10 most abundant in each lake: *Chydorus sphaericus*, *Alona rectangula*, *Acroperus harpae*, *Eurycercus lamellatus*, *Camptocercus rectirostris*, *Graptoleberis testudinaria* and *Alona affinis*. Perhaps these species tolerate a wide range of ecological conditions, but it is interesting that with the exception of the first two listed, all are among the largest chydorids, and this could be favoring their recovery. These same seven are among the ten most abundant species that Frey (1960a) found in the Madison lakes, eight of which would be considered "large" chydorids.

To say that any sediment sample will yield a chydorid percentage composition characteristic of all surficial sediment from a lake is only partially true, since some variation in percentages and rank order is found among the samples. Yet it is possible to obtain from any sampling site a fairly accurate approximation of the relative abundance of species. Frey (1958, 1961a) points out that when interpreting cladoceran ecology or lake ontogeny through the use of cladoceran microfossils, the mere occurrence of individual species is not adequate, but a better understanding of conditions is gained by considering species assemblages and the relative abundance or rank order of these groupings. The data obtained in this study indicate that a sample from any location in a lake should prove adequate for this purpose, since the transport of remains offshore is not selective. If a certain size group of remains or species is being differentially transported, it is of such low magnitude that the present methods cannot detect it.

THE LITTORAL-PLANKTONIC RATIO

The species comprising the littoral and planktonic categories were listed in the Ecology section. The littoral group consists of substrate associates, few of which dwell in numbers beyond the littoral area. All open-water Cladocera are assigned to the planktonic group. The change in relative proportion between these groups with increasing depth and distance from shore is potentially useful in deciding the influence of

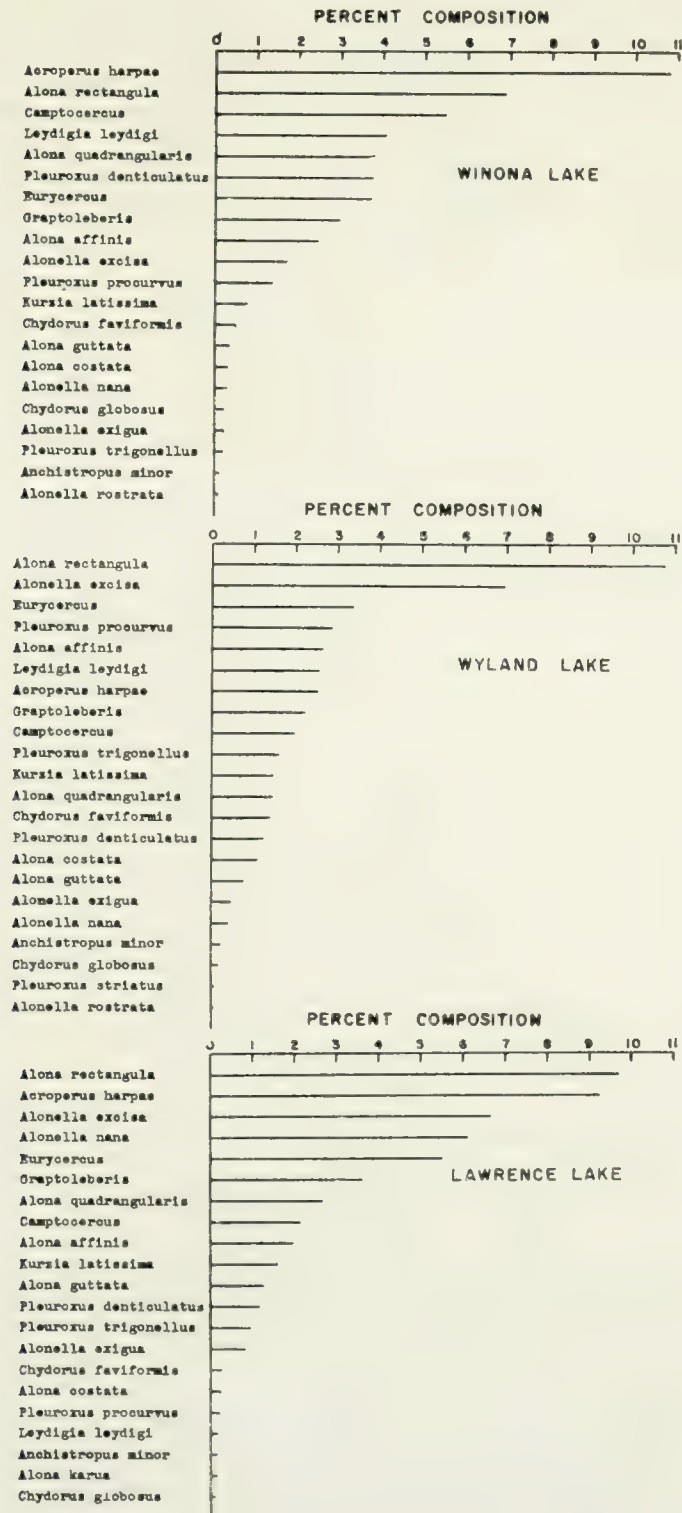


TABLE 12. Chydorid species abundance obtained by combining all samples from each of the three lakes.

redemption on the composition of the sedimented cladoceran remains. The littoral-planktonic percentage curve for the west-to-east transect of Wyland Lake (Fig. 20) displays the characteristic pattern shown by all transects. With increasing depth and distance from shore the littoral

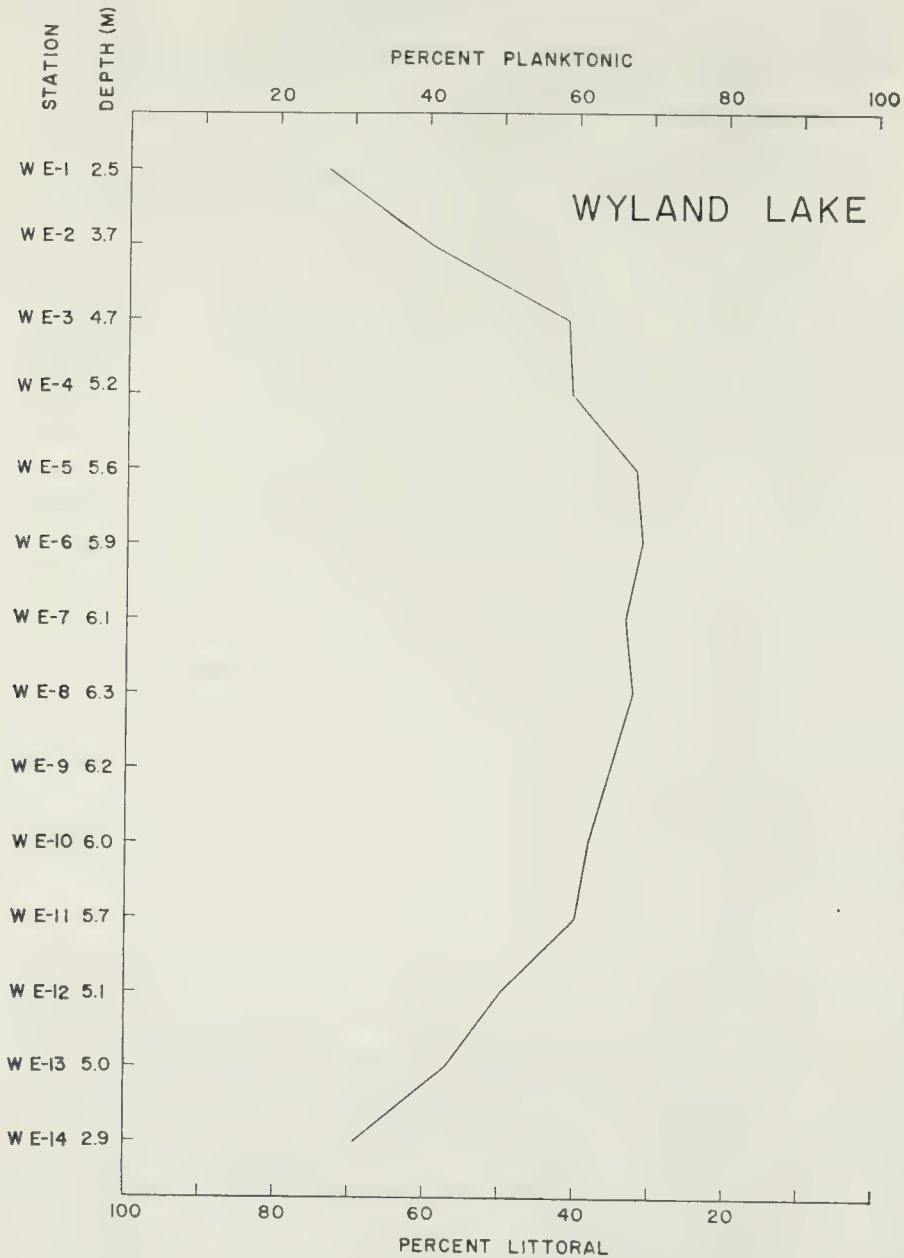


FIG. 20. Littoral and planktonic percentages for the west-to-east transect of Wyland Lake.

percentage decreases, and the planktonic percentage increases. After the initial decline, which is always quite marked where the sediments contact epilimnetic or metalimnetic waters, there is a marked leveling off that continues to the deep end of the transect.

This same pattern is found when the non-transect data of Winona (Fig. 21) are plotted against increasing depth. Again there is a shoreward high in littoral remains followed by a decrease and then stabilization. Notice that SS-7, -15, and -4, which distorted the expected relationships in the CaCO_3 curve, also disrupt the smoothness of this curve. The probable cause of their lack of conformity will not be considered again, but it is interesting to speculate that the high littoral value at

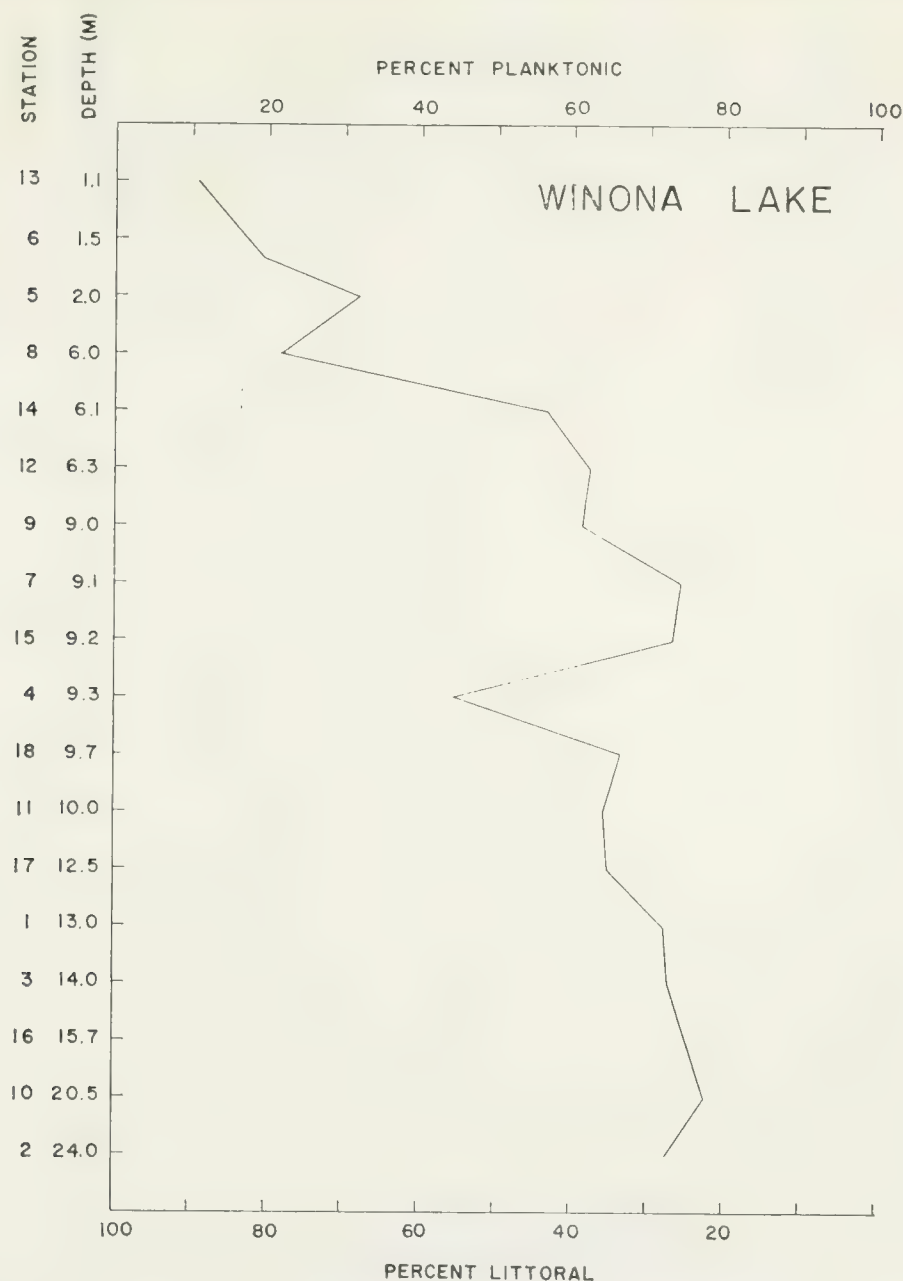


FIG. 21. Littoral and planktonic percentages for the non-transect samples of Winona Lake arranged in order of increasing depth.

SS-4 results from the relatively close littoral zone—the shore is only 100 m away.

The percentages from the Winona transect (Fig. 22) show the same general pattern, with the exception of a significant increase in littoral remains at the deep end of the transect. (Samples T-3 through T-6 compared with T-7 through T-10 give a “t” value of 6.434 with 6 d.f.) This increase is attributed to higher fragmentation of chydorid remains in the deeper samples. This point will be discussed in the next section.

To complete the presentation for the three lakes, similar data for the west transect of Lawrence are shown in Figure 23. The usual decline in

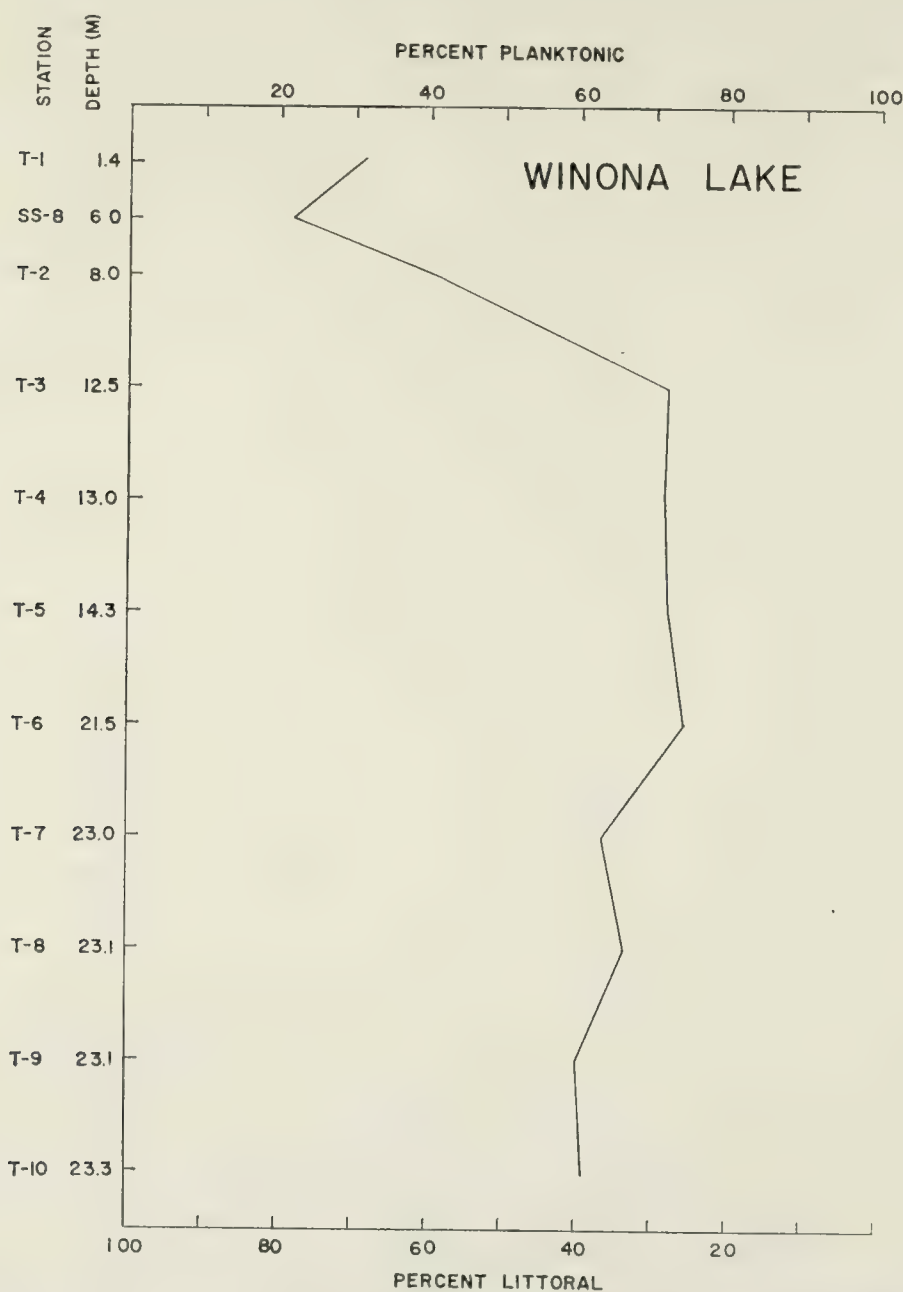


FIG. 22. Littoral and planktonic percentages for the Winona transect.

littoral remains offshore occurs, and in the hypolimnion only minor fluctuations occur between the two proportions.

The form of the littoral-planktonic curve results from the discreteness of these two cladoceran habitats, the direct deposition of remains in their respective zones, and the subsequent redeposition of remains. It is primarily the latter factor that produces the characteristic distribution. Were it not for redeposition, the littoral remains would stay inshore and the planktonic remains would be spread fairly evenly over the lake floor, except for a decrease toward the shoreward area. Through water movements the remains in the littoral area are transported and redeposited offshore, but the magnitude of the transporting agent diminishes below the metalimnion. The curve levels off in the upper hypolimnion where the

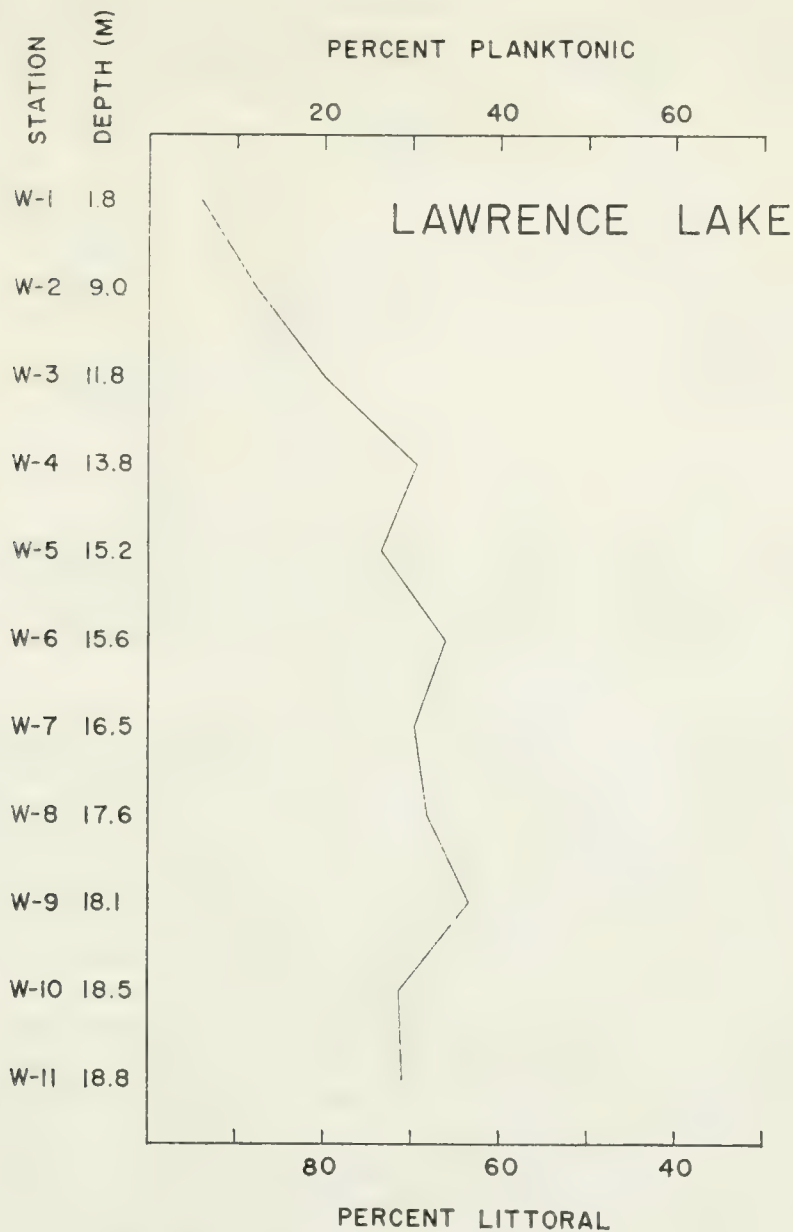


FIG. 23. Littoral and planktonic percentages from the west transect of Lawrence Lake.

basin slope diminishes and where the effects of surface water movement are substantially reduced. From the results presented in the previous two sections, it is important to emphasize that the off-shore redeposition of littoral remains is not a selective process that changes the relative abundance of chydorids. Apparently the chydorid remains are thoroughly integrated in the littoral zone before being transported offshore. Yet, as will be shown, the absolute number of remains per unit sediment changes appreciably.

Frey (1960a: p. 698) states "the percentage composition of the microfossil population appears closely related to that of the producing population, and also appears to be closely related to the morphometry of the lake." He postulates that an increase in substrate organisms may be used

TABLE 13. Morphometric data and metalimnetic limits for Carr, Crooked, and Pleasant lakes. All measurements except the last were obtained by the writer from maps prepared by the U.S.G.S. and the Indiana Department of Conservation.

	Carr	Crooked	Pleasant
Area (ha)	32.0	76.6	20.8
Volume ($\text{m}^3 \times 10^6$)	1.47	11.1	1.39
Maximum depth (m)	10.7	33.0	13.4
Mean depth (m)	4.6	13.3	6.8
Mean/maximum depth	0.430	0.403	0.507
Length of shoreline (m)	2534	5760	2290
Shoreline development	1.26	1.78	1.42
Metalimnetic limits (m)	3-8	5-11	6-10

to indicate a shift from planktonic to littoral production, or vice versa, and Brehm *et al.* (1948) have used the relative abundance of chydorid and planktonic species to indicate periods of expansion and contraction of lake area. The data obtained in the course of this study seem sufficient for an inquiry into this relationship.

Percentage composition data are available from Wyland, Winona, and Lawrence lakes, plus a single analysis each from near the deepest location of Carr, Crooked, and Pleasant lakes, located in Kosciusko, Noble-Whitley, and Steuben counties, respectively. These six lakes are all located in northern Indiana near $41^\circ 21' \text{ N}$. Morphometric data for the latter three lakes are presented in Table 13. For reasons deferred until the Discussion, the littoral-planktonic percentages from the deepest sample available from each of the six lakes was used for comparison. All lake maps were planimetrically measured for the determination of (1) the area of the littoral zone floor, the limits of which have been arbitrarily defined as the shore line and the place where the top of the metalimnion intersects the lake bottom, and (2) the volume of the planktonic zone, defined as all water from the lake surface to the bottom of the metalimnion exclusive of water overlying the littoral floor just defined. The avoidance of shore response of certain zooplankters seems to justify this exclusion. From these two measurements a ratio of planktonic volume (m^3) to littoral area (m^2) was obtained for each lake (the P/L ratio). The lower this value the greater should be the influence of littoral production. Plotted against each ratio in Figure 24 is the littoral-planktonic percentage of cladoceran remains for that lake. Perhaps the compensation level or the lower extent of rooted aquatics would serve as a better limit for the offshore littoral boundry, but unfortunately these data are not available, and their collection would require the integration of results obtained during several years study. Although these limits are arbitrary, the P/L ratio does not appreciably change by small shifts in the limits as long as the contour lines are close together.

Figure 24 relates the littoral-planktonic percentages and the P/L ratio. Line A was fitted by least squares to the data for the six Indiana lakes. The close correlation between these two variables is indicated by a correlation coefficient of 0.95 with 4 d.f. The 1% level of significance is 0.917. The available evidence for these lakes indicates that the ubiquitous

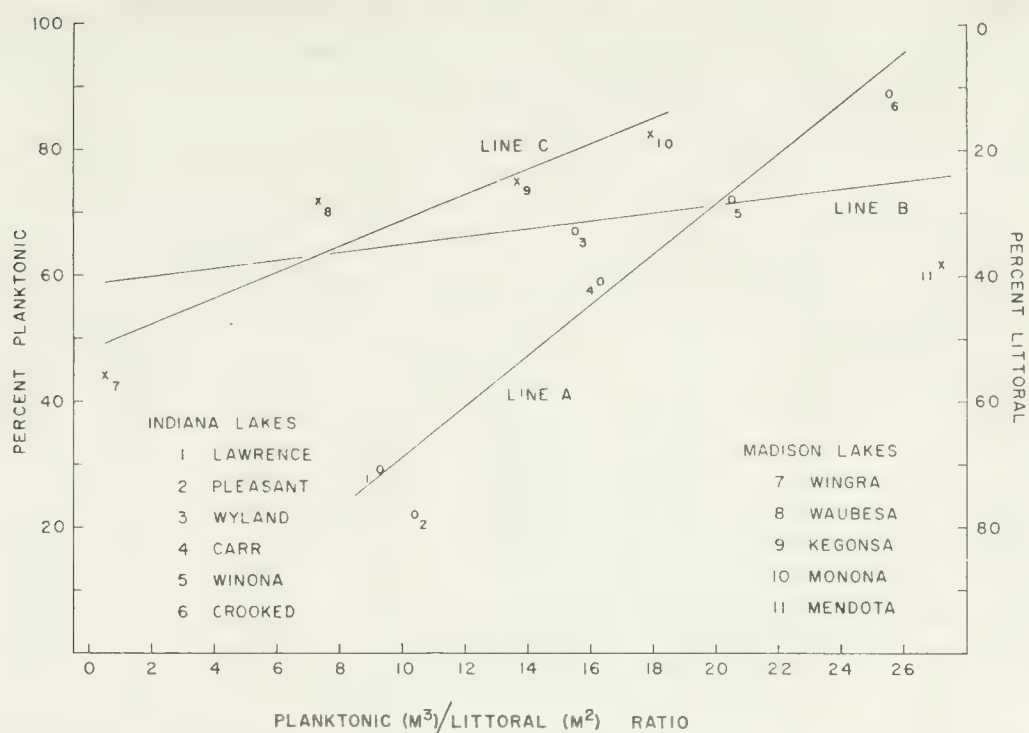


FIG. 24. Regression lines for the littoral and planktonic cladoceran percentages plotted against the P/L ratio.

Line A—Six Indiana lakes

Line B—Madison lakes

Line C—Madison lakes, Mendota excluded

$$\text{Equation: } y = -6.92 + 4.02x$$

$$\text{Equation: } y = 58.44 + 0.65x$$

$$\text{Equation: } y = 48.90 + 2.05x$$

Chydorus sphaericus is almost entirely a littoral inhabitant with only minor representation in the plankton. It is apparent that the relative proportion of littoral and planktonic remains in deep-water sediments is closely related to the P/L ratio. As littoral area increases relative to planktonic volume, there is a corresponding increase in littoral Cladocera reflecting an increase in the substrate-type of habitat necessary for a littoral fauna. Thus, small lake size does not necessarily indicate an extensive shallow-water zone relative to the planktonic zone. The littoral percentage in Wyland and Lawrence lakes are 33% and 71% respectively. Although Lawrence is eight times larger than Wyland its higher littoral representation reflects a more extensive shallow-water area.

Attempts to correlate the littoral-planktonic percentage with area, mean and maximum depth, and volume were unsuccessful.

An additional comparison between this percentage and the P/L ratio can be made with the data of Frey (1960a) from the five Madison lakes where *C. sphaericus* is an abundant plankter. Table 14 shows some of the inverse percentage progressions of cladoceran constituents between the Madison and Indiana lakes. Both series of lakes are arranged in order of their increasing P/L ratios, and for each group opposite trends are shown for all constituents except "Other chydorids." Mendota, which is three times larger than the next smallest of the five, is out of place with respect to *C. sphaericus* and "Other chydorids." Frey explains the high in "Other chydorids" as fragmentation of exuviae, possibly by a large population of offshore benthos.

TABLE 14. Percentage composition of several cladoceran components from deep-water sediment of six Indiana lakes and the Madison lakes related to the P/L ratio. The Madison lake ratios were determined from morphometric data in Pearse and Achtenberg (1920) for Wingra and Juday (1914) for the other four. Percentages, areas, and mean depths for the Madison lakes are from Frey (1960a).

Lake	Area (ha)	Mean depth (m)	P/L ratio	Percentage composition			
				<i>Bosmina</i>	<i>Chydorus</i> <i>sphaericus</i>	<i>Daphnia</i>	Other chydorids
Wingra	81	1.6	0.0	42.9	22.7	1.2	33.2
Waubesa	824	4.9	6.8	16.9	55.6	6.2	20.9
Kegonsa	1273	4.6	13.1	8.5	65.4	5.4	20.2
Monona	1410	8.4	17.4	5.2	67.8	13.3	13.1
Mendota	3940	12.1	26.7	3.3	43.8	16.3	36.6
Lawrence	27.4	7.0	8.8	9.3	31.1	19.5	38.9
Pleasant	20.8	6.8	9.9	0.3	29.4	21.7	46.9
Wyland	3.4	3.8	15.0	64.1	16.0	3.5	16.3
Carr	32.0	4.6	15.8	54.8	14.5	4.4	26.0
Winona	203.7	9.1	20.0	66.4	11.9	4.4	14.1
Crooked	76.6	13.3	25.0	87.3	3.2	0.6	6.9

No explanation can be offered for the contrary cladoceran progressions, but in the Ecology section it was mentioned that the assignment of Cladocera to a strictly littoral or planktonic habitat cannot always be made with certainty.

The planktonic percentages in these lakes must take into account the contribution of open-water *sphaericus* remains. This was done by arbitrarily separating their number for each lake into littoral and planktonic categories based upon the P/L ratio. By definition Wingra is completely littoral and all *sphaericus* must be assigned to this category, although Pearse and Achtenberg (1920) showed that not all of the fauna of Wingra are substrate associates. For this reason, a P/L ratio slightly above zero would be more realistic.

The adjusted percentages do not fall along regression line A but rather along regression line B (Fig. 24), whose correlation coefficient of 0.45 with 3 d.f. is not significant. Since Mendota does not conform to the other four lakes in its *C. sphaericus* and "Other chydorids" percentages, a line was drawn excluding Mendota. This is line C, whose correlation coefficient is 0.93 with 2 d.f. The 5% level of significance is 0.95. A comparison of lines A and C shows that the planktonic representation in the Madison lakes is at a higher level than in the Indiana lakes due to the contribution of *sphaericus* from both littoral and planktonic zones. Also, there is a greater planktonic representation at a lower P/L ratio in the Madison lakes than in the Indiana group and an increased percentage of *Bosmina* as the P/L ratio declines.

The relationship between the littoral-planktonic percentage and the P/L ratio should be useful to the paleolimnologist as an indicator of the areal changes between the shallow-water and open-water zones. The relationship appears valid provided the littoral and planktonic components are discrete or that some disposition is made of members inhabiting both

zones. An alternative might be to eliminate from consideration those occurring in both zones and work with the remaining ones.

FRAGMENTED AND NON-FRAGMENTED REMAINS

Every effort was made during the slide preparation to handle all sediment in the same manner so that any breakage of remains introduced by treatment would be constant for every sample. In this way, any differences in breakage between collection sites is a function of conditions in the lakes.

The percentages of broken and intact remains of *Bosmina*, Chydoridae, and the total of *Bosmina* + Chydoridae are shown in Figure 25 for the Winona transect and in Figure 26 for the west-to-east transect for Wy-

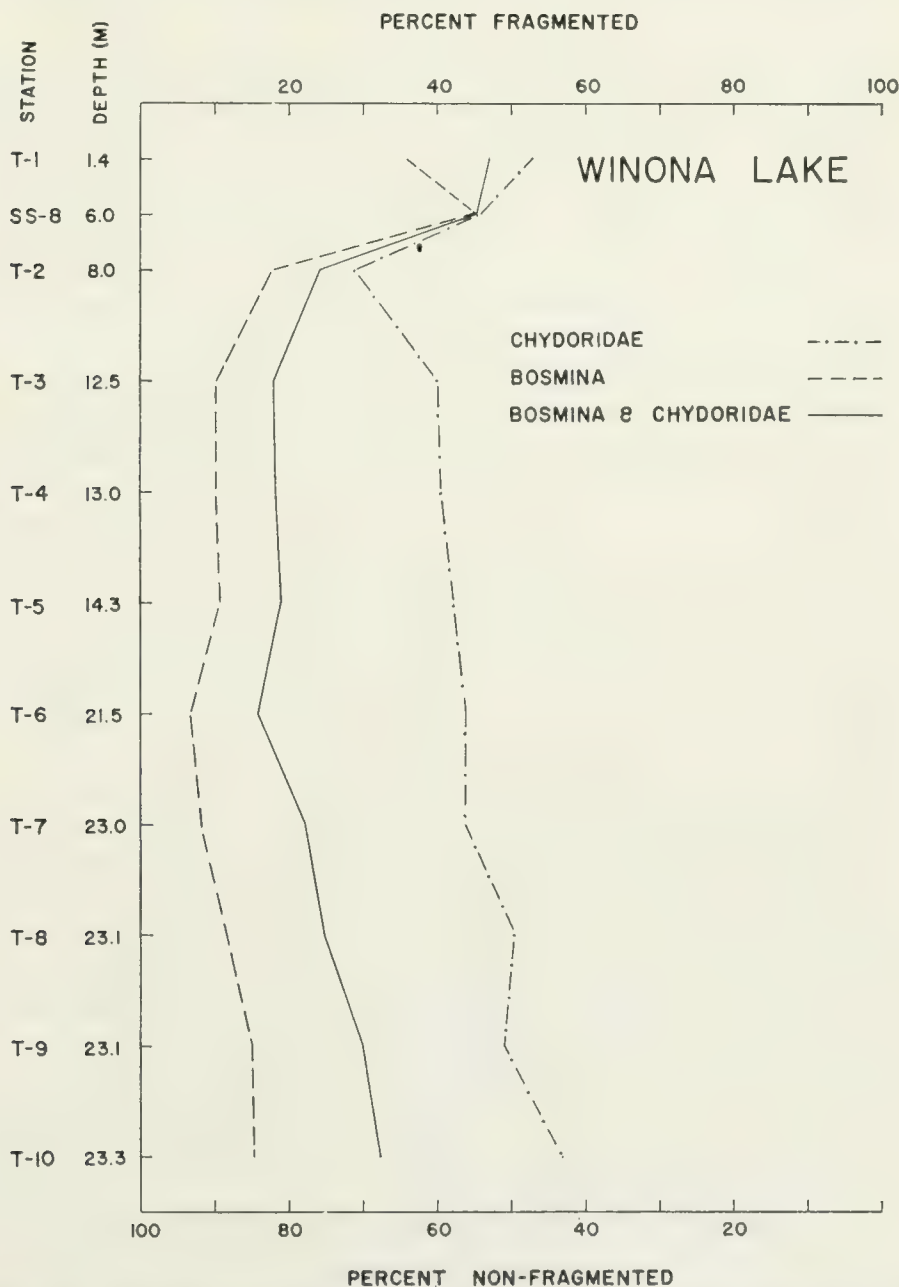


FIG. 25. Percentage of fragmented and non-fragmented remains. Winona transect.

land. Although data from the Lawrence Lake transects are omitted, similar distributional patterns were found in all three lakes. Offshore the chydorids are considerably more fragmented than *Bosmina*, while inshore the two percentages are similar where remains and other bottom materials are being shifted by currents and turbulence. Acton (1916) reported "undulatory movement" at 4 m sufficient to roll *Cladophora* into packets that increase in size towards 1 m where *Cladophora* balls are found in quantity. Such mechanical action conceivably could break almost any cladoceran remain. The offshore chydorid remains must reflect the fragmented condition of those in shallow-water because of the offshore movement. Offshore *Bosmina* remains, while possibly derived in small part from the shallow water, primarily result from sedimentation of exuviae from plank-

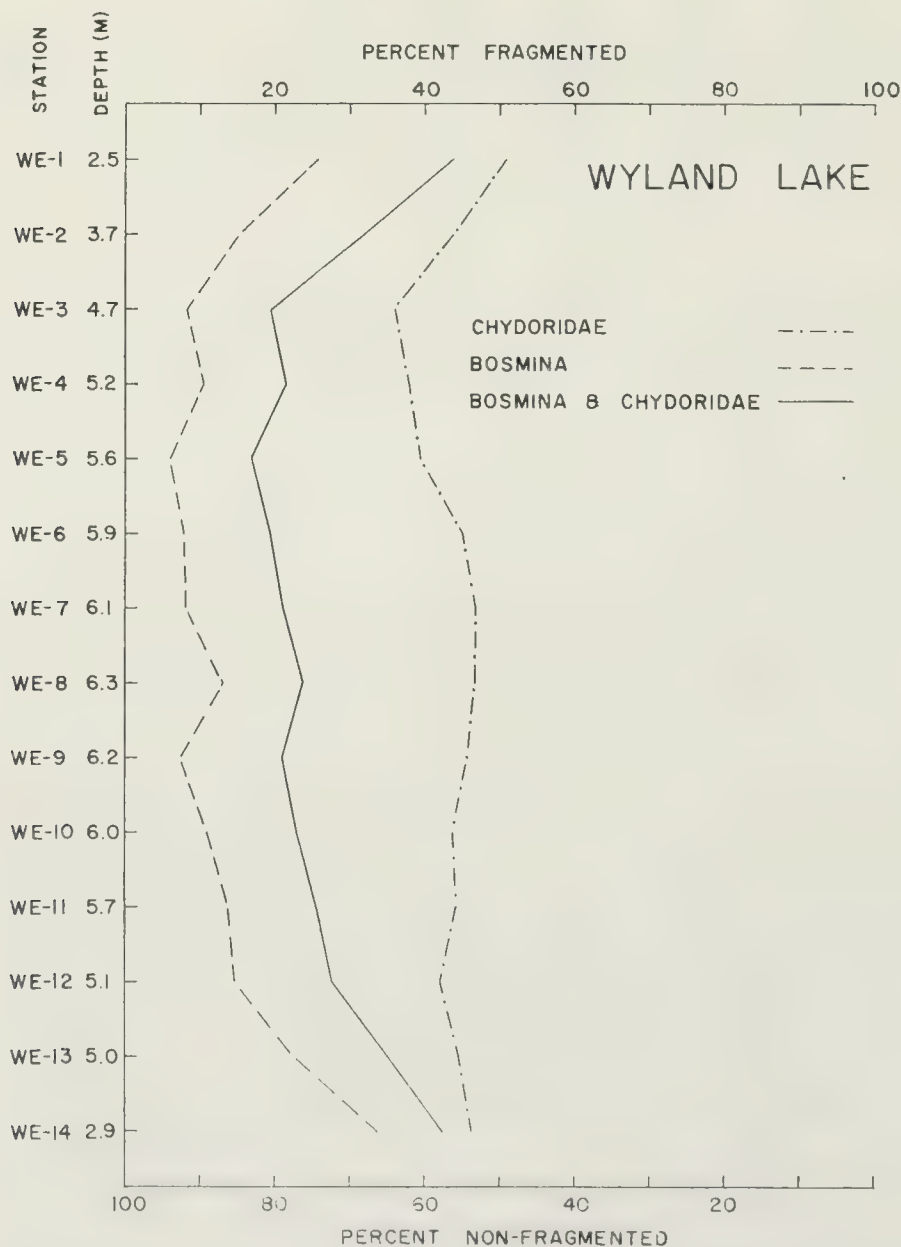


FIG. 26. Percentage of fragmented and non-fragmented remains. West-to-east transect, Wyland Lake.

ters, and once deposited they are not subjected to breakage forces comparable to those in shallow areas. If the feeding activities of the benthos are responsible for the breakage of offshore remains, then the percent of fragmented *Bosmina* and chydorids should be similar, but the wide separation between the percentages seems to eliminate this possibility.

In Lower Linsley Pond, Vallentyne and Swabey (1955) consider the deep-water breakage zone (ca. 7500 B.P.) to be the result of mechanical breakage because of the diversity of broken biota (pollen grains, statoblasts, and diatom tests). After experimentally subjecting *Bosmina* remains to grinding and shaking action, Vallentyne and Brown (1957) proposed that the zone results from breakage inshore with subsequent displacement offshore of the broken parts, and that turbulence (and consequent grinding) at the offshore mud-water interface is an untenable explanation of the observed breakage.

Fragmentation of remains must also be considered by combining the mechanical breakage just discussed with chemical and biological factors inherent in inshore and offshore sediments. Great differences between these two regions might be expected *a priori* merely on the basis of the partial to complete anaerobiosis experienced by the deep-water region for extended periods. This difference in oxygen alone can account for many chemical and biological differences between inshore and offshore water and sediment. For example, a different complex of bacteria between the two regions could be expected, and their action upon chitin might confer to a remain an increased resistance or susceptibility to subsequent mechanical action. Likewise, the pH of the sediment, even if without a direct effect upon chitin, can certainly influence other chemical and biological events that might modify these remains.

There is an increase in fragmented remains at the deep end of each transect. The increase in chydorid fragments in Winona is possibly the explanation for the higher littoral percentage at a similar region in Figure 22. An attempt to explain this deep-water increase in fragments will be mentioned in the next section.

QUANTITATIVE DISTRIBUTION ALONG TRANSECTS

The previous analyses have shown the relative abundance of various cladoceran components and the species present. Now the absolute abundance will be related to a specific quantity of sediment. It is necessary for this purpose to select a stable and conservative sediment parameter showing a minimum of post-depositional change. This immediately eliminates CaCO_3 , since its reaction with CO_2 can result in great differences between inshore and offshore sediment, even if its deposition were equal over the entire basin. Furthermore, if CaCO_3 were used it would be impossible to make comparisons with non-calcareous lakes. This also eliminates total dry weight when CaCO_3 is present in the sediment.

The parameter used in the following presentation is composed of the two most stable components determined in the chemical analyses—residue and organic content. This parameter, which is merely total dry weight less calculated CaCO_3 , is a conservative approach to the original dry weight of sediment.

For each transect the number of remains/g organic + residue are presented for the following cladoceran groupings: total remains, littoral, *Chydorus sphaericus*, Other chydorids, planktonic, and *Bosmina*. To simplify the description of these many curves, the Winona transect (Fig. 27) will be considered first to form a frame of reference for the others.

Littoral remains in Winona decline rapidly with increasing distance from their zone of production, with a plateau interrupting the curve in the upper hypolimnion. *C. sphaericus* and Other Chydorids follow the same pattern, and both have a similar quantitative representation, since *sphaericus* composes about 50% of all chydorids. Planktonic remains and the dominant plankter *Bosmina* are low inshore, increase rapidly to a plateau in the upper hypolimnion, and abruptly decline before stabilizing at the

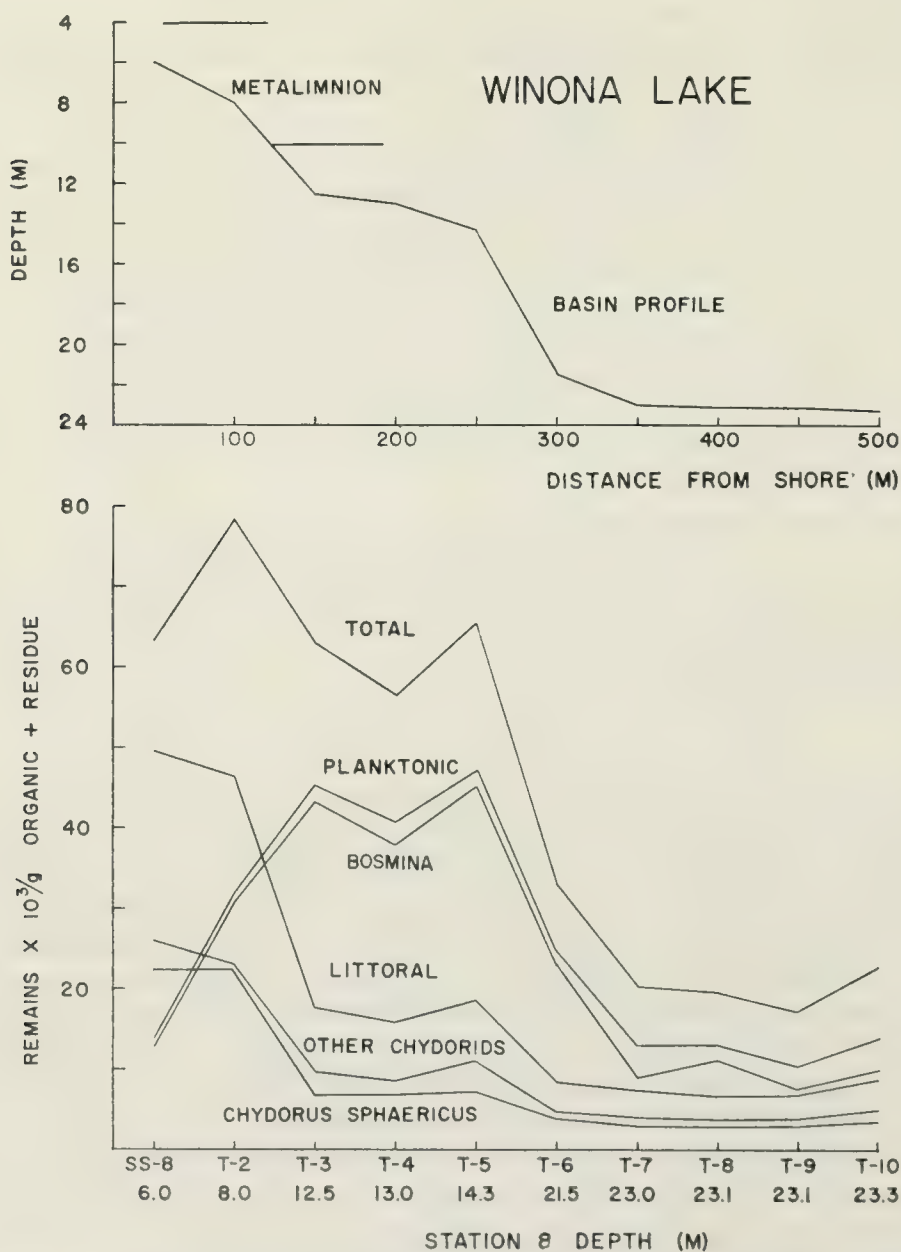


FIG. 27. Basin profile, metalimnetic limits, and the quantitative distribution of remains/g organic + residue along the Winona transect.

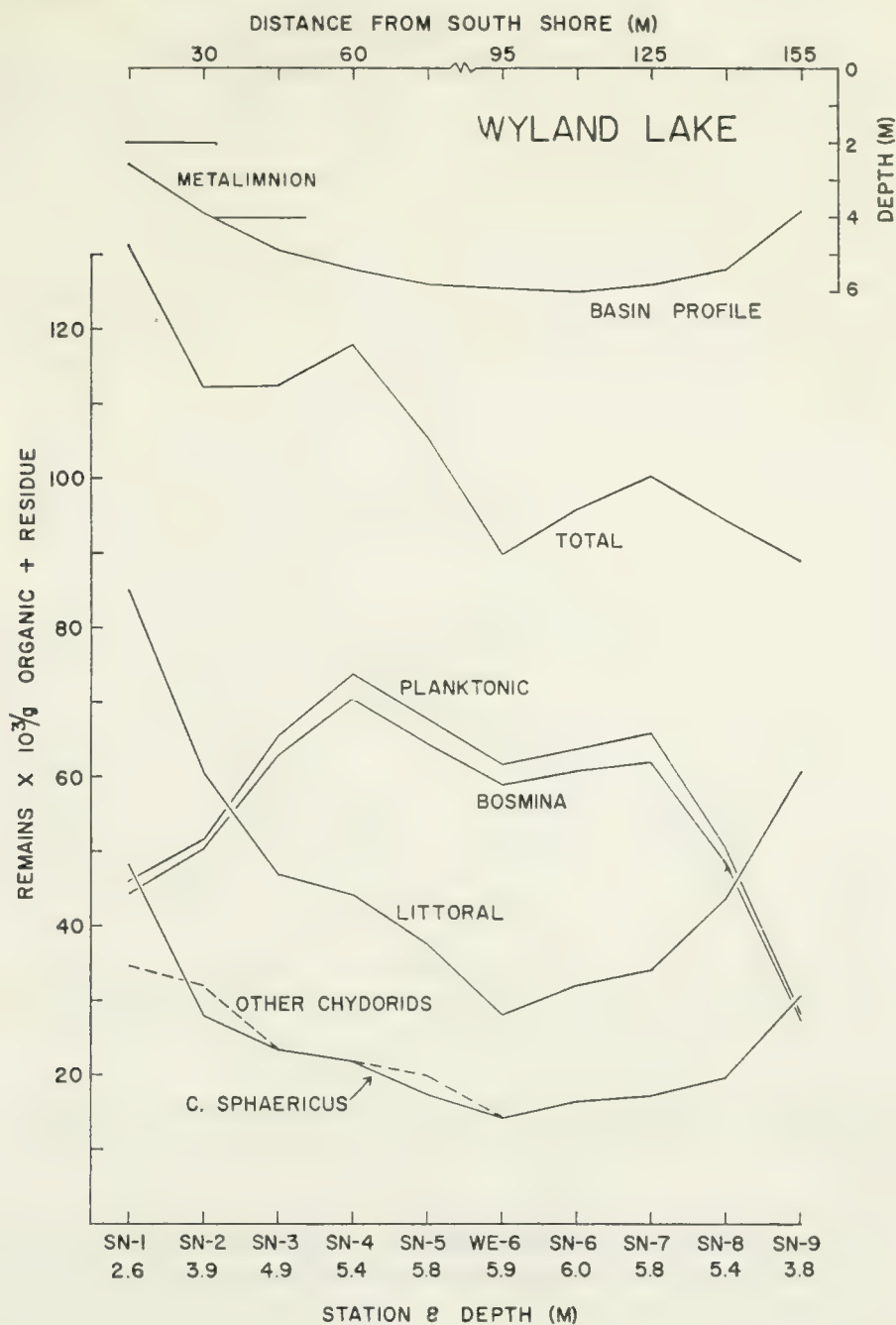


FIG. 28. Basin profile, metalimnetic limits, and the quantitative distribution of remains/g organic + residue along the south-to-north transect of Wyland Lake.

far end of the transect. This is excellent evidence that offshore as well as inshore remains are subject to post-depositional movement. A reasonable expectation is a uniform contribution of planktonic remains over the open-water with a decline toward shore, but this peak or "concentration zone" is found in all transects and usually in the upper hypolimnion. The curve for total remains declines from shore to deep water with an interruption in the upper hypolimnion. The lower value near shore could possibly be due to dilution by allochthonous material or aquatic macrophytic detritus.

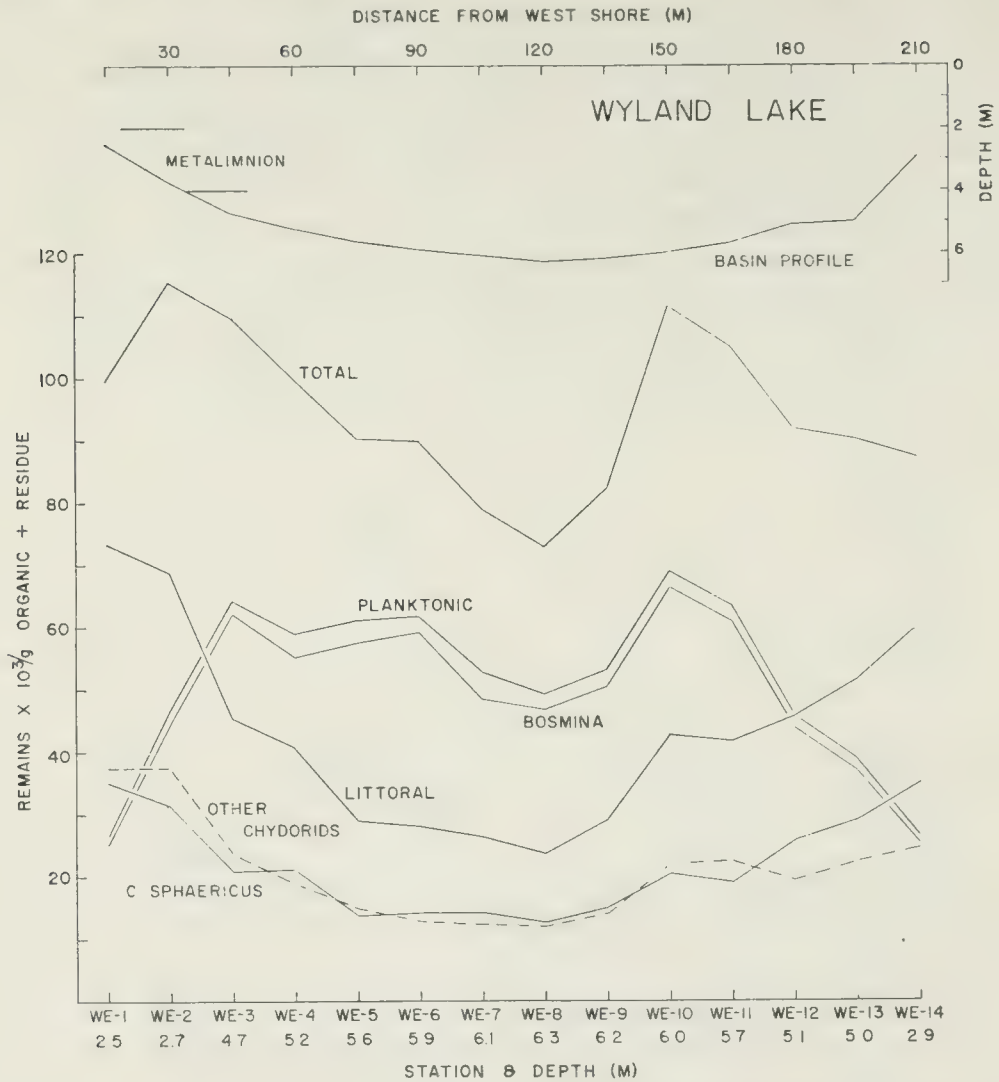


FIG. 29. Basin profile, metalimnetic limits, and the quantitative distribution of remains/g organic + residue along the west-to-east transect of Wyland Lake.

The two transects from Wyland Lake (Figs. 28 and 29) are similar to that of Winona but with these differences. The decline following the planktonic and *Bosmina* peak is not so well marked as in Winona, probably resulting from a lesser depth and distance beyond the concentration area. The south and west transects show an almost continuous decline in total remains. The low values along the north transect, however, are attributed to the narrow littoral zone, which reduces the space available to substrate Cladocera. The depression of total remains near the east shore is caused by dilution from materials washed in from farmland that lies beyond the wooded shore.

The south and north transects of Lawrence (Fig. 30) have been presented as a single traverse extending from shore to shore. The west transect is shown in Figure 31. *Daphnia* is the dominant plankter in the lake, which accounts for the wide offshore difference between *Bosmina* and planktonic remains. The low values in the south bay result from dilution by abundant vegetation. The highest organic values (based on total sediment)

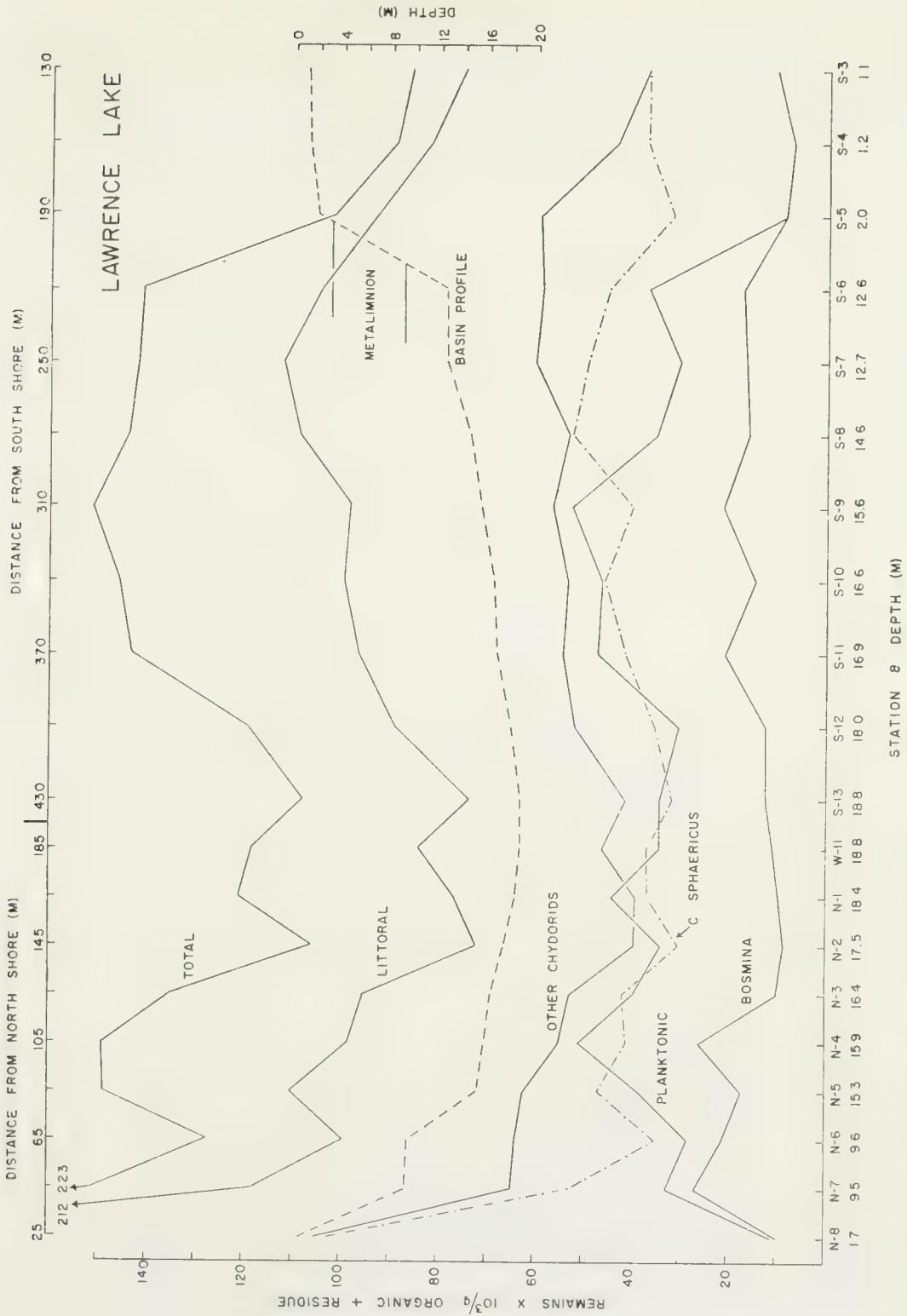


FIG. 30. Basin profile, metalimnetic limits, and the quantitative distribution of remains/g organic + residue along the north and south transects of Lawrence Lake.

were found here, and even with the increased substrate available for Cladocera the bay is so choked with vegetation that the remains are diluted. Low values near the west shore are the result of dilution by materials washed in from a cleared watershed, part of which is now a public access site.

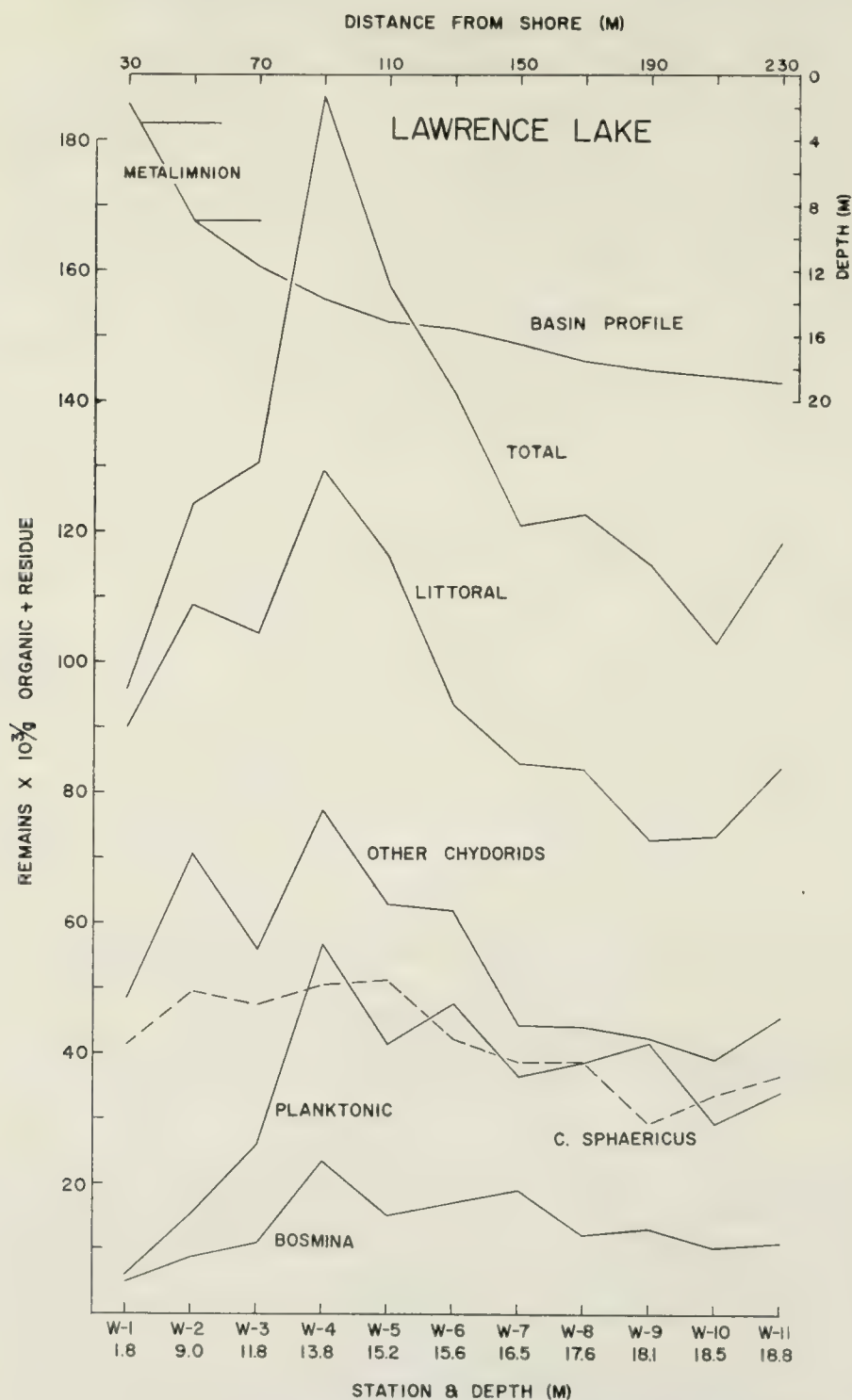


FIG. 31. Basin profile, metalimnetic limits, and the quantitative distribution of remains/g organic + residue along the west transect of Lawrence Lake.

The non-transect samples from Winona (not shown) when arranged in order of increasing depth show the same quantitative distribution of remains as the transects, but the inshore values are very low. An offshore peak is present in all samples between 6.3 and 12.5 m. This quickly de-

clines to a uniform level below 13.0 m. Again the curves are distorted by the same four samples previously discussed.

Although not presented, the curve for total remains/cc wet sediment from every transect shows a well-marked offshore peak, with a rapid decline towards shore and deeper water and a range of 1000 to 12,000 remains/cc. The water content of sediment can be altered during collecting, but since the same method was used for each dredge haul these curves are considered reliable.

In explaining these distributional patterns it is necessary to mention briefly several conditions bearing on this problem.

(1) The littoral Cladocera are a fairly discrete group primarily restricted to inshore areas where their remains would be localized were it not for redeposition.

(2) It seems reasonable that planktonic remains would be uniformly distributed with a decline only towards shore, and that no major accumulation could occur without redeposition. On the other hand, a concentration might result if non-cladoceran sediment constituents were removed from a given region.

(3) The occurrence of a cladoceran bottom fauna below the littoral zone was discussed earlier. It is doubtful that such Cladocera could produce a major accumulation of sublittoral remains.

(4) Reference to Figures 25 and 26 shows that an accumulation of fragmented remains is not responsible for any peak in offshore remains.

(5) There is a gradient of decreasing sediment particle size ranging from coarse near shore to fine over the central plain, a phenomenon amply shown by Kindle (1930), Reissinger (1932), and Twenhofel (1933) among others. This gradient results from a general but not uniform decrease in current velocity and transporting power with increasing depth, resulting in sedimentation of progressively smaller particles. Likewise, with increasing depth the ability of erosional agents to remove sediment favors the smaller particles.

The most noticeable feature in nearly every transect is the transitional character of the curves in the upper hypolimnion shown either by a peak in the number of remains or by some type of interruption of the trend. As mentioned above, the form of the curves cannot be attributed to either fragmentation or the habitation of offshore sediment by living Cladocera.

It is necessary then to examine the post-depositional agents—primarily currents and turbulence and their possible influence on the distributional patterns. These agents, if of sufficient magnitude, can dislodge sediment particles and transport them, usually downslope, since the water's density is increased by a suspended load. The transitional features noted in the upper hypolimnion suggest that here there is a loss of current velocity and, therefore, transporting power. This agrees with Lathbury *et al.* (1960), who found that mean maximal current velocities in Mendota occur at the surface and bottom with minimal velocities in the middle and upper hypolimnion. At this level, erosional forces are sufficient to partially remove the smaller silt and clay size particles while leaving behind the remains that are now somewhat more concentrated by this removal. In deeper water

with diminishing transporting power, this load is deposited causing a dilution of the remains at these deeper locations. That these erosional forces also remove the small fragmented cladoceran remains is suggested by the slightly increased proportion of such remains at the deep end of the transects (see p. 45). This series of events increases the quantitative difference between remains in the upper and lower hypolimnion.

The offshore gradient of littoral remains shows that fewer and fewer are transported to sites progressively more distant from their zone of production. Thus, each subsequent removal, transport, and deposit involves fewer remains than the preceding event.

The quantitative distribution is an integration resulting from habitat differences, the passive transport of remains and their sedimentary matrix, and in certain locations the addition of allochthonous material. These events are operating within the framework of thermal stratification. The sediment collector study considered next shows that during overturn deep-water sediment is brought into circulation. But these disturbances of sediment do not erase the distributional patterns established during stratification.

THE SEDIMENT COLLECTORS

Introduction

Previous studies on the accumulated sediment in collecting vessels have not been concerned with Cladocera or their chitinous exuviae. In fact, the only mention even given to Cladocera is Reissinger's (1932) finding of "Reste von Bosminen" in collecting vessels. Scott and Miner (1936), collecting sediment in Winona Lake, found many organisms much smaller than cladocerans but do not mention living Cladocera or their remains. *Paramecium caudatum* was found in a collector at 24 m by Thomas (1950), whose study was largely of a chemical nature. Tutin (1955) could not regard the sediment collected at 14 m in Windermere a reliable quantitative estimate because of "so many animals," but no names are given.

Early collector studies dealt with the rate of sedimentation and the nature of the deposit. Scott and Miner (1936) studied the influence of the marl knobs in Winona on nearby sedimentation. Chemical analyses were made, and the relative abundance of algae in the vessels was noted. Reissinger (1932) set out collectors along transects extending from the inlet to beyond the central plain in narrow valley lakes and integrated the sedimentation rate over a period of from $2\frac{3}{4}$ to 8 years. In Starnberger See he observed annual layers that corresponded exactly to the years ($2\frac{3}{4}$) of sedimentation. Although a collector was not employed, Fehlmann and Minder (1921) recorded sedimentation rates on a submerged conduit in Zürichsee. Tutin (1955) studied a year's cycle of sedimentation in Windermere and correlated planktonic *Asterionella* with the sedimentation rate and diatoms in the surficial sediment. Grim (1950, 1952) determined diatom production by collecting the individuals falling through a given stratum of water. In later studies Kleerekoper (1953) has been concerned with nutrient cycling, and Thomas (1955) has attempted to characterize oligotrophic and eutrophic lakes in relation to nutrient cycles.

The purpose of this collector study was to determine the time of re-deposition of littoral remains into offshore locations and the strata of water involved if this occurred during stratification, and to determine the composition of cladoceran remains in sediment that accumulated in the various vessels during fall overturn. Since Tutin (1955) found a "mature" sediment in her collectors during fall overturn, a favorable comparison might be expected between remains in the vessels and in the adjacent surface sediment. Eggleton (1931) suggested that during overturn, currents of sufficient velocity to move a varied collection of shoreward debris to deeper levels might also distribute littoral organisms and disperse the profundal benthos. He makes no mention of Cladocera or their exuviae in his collecting vessels.

Results

Pertinent information on the collector series is given in Table 15. Each series was installed and removed during stratification with the exception of Series 2 and W-4, which were removed after the onset of fall overturn that began about mid-October.

Sufficient sediment usually accumulated in the vessels during the span of 1 to 2 months for an analysis of chemical components and cladoceran remains. If the sediment volume was low the entire amount was used for a quantitative analysis.

TABLE 15. Pertinent information on the sediment collector series from Winona Lake.

Series number	Year	Duration	Days in water	Lake depth at collector site (m)	Depth of vessels (m)
1	1959	Aug. 3-Sept. 27	55	14.9	1.8 3.8 6.8 9.8 11.8 13.8
2	1959	Sept. 27-Nov. 7	42	14.7	1.8 3.8 6.8 11.8 13.8
3	1960	May 28-June 29	32	16.1	14.1
W-2	1961	June 28-Aug. 14	47	15.2	8.0 14.0
W-4	1961	Sept. 14-Nov. 13	59	15.2	3.0 8.0 11.0 14.0

TABLE 16. Cladocera found living in the collector vessels of Series 1 (stratification) and Series 2 (overturn) in 1959.

	Depth (m) and series number					
	1.8	3.8	6.8	9.8	11.8	13.8
	1 2	1 2	1 2	1 2	1 2	1 2
<i>Sida crystallina</i>	x o	x	x o			
<i>Bosmina longirostris</i>	o	x o	o	o	o	o
<i>Ilyocryptus spinifer</i>	x		x			
<i>Camptocercus rectirostris</i>	x o					
<i>Acroperus harpae</i>	o					
<i>Graptoleberis testudinaria</i>		o				
<i>Leydigia leydigi</i>	o		x	o		o
<i>Alona guttata</i>	x o					
<i>Alona rectangula</i>	x o	x o	x o			
<i>Pleuroxus denticulatus</i>	x o	o				
<i>Chydorus sphaericus</i>	x o	o				

Collector designs and sediment preparation have been discussed in the Methods section. Collector locations are indicated on the Winona map (Fig. 1).

1. *Colonization of the collector vessels.* Vessels in the epilimnion and photic zone developed a living population of substrate-associated Cladocera and a secondary growth of algae. For this reason, the fresh sediment was examined for living Cladocera. If these were at all abundant the quantitative analysis was questioned, since their contribution of exuviae would be included with sedimenting remains, resulting in excessive numbers and erroneous proportions. Table 16 shows that during stratification only the uppermost three vessels of Series 1 were colonized, while after overturn in Series 2 at least one species was found at each depth. It was necessary for the littoral species to pass through open-water to the vessels. Nine species of littoral Cladocera were recovered alive in the plankton, but these were rare occurrences. The number of organisms in the lowermost three vessels was quite small, and their alteration of the collected sediment would be minor. For this reason, vessels positioned in the hypolimnion and lower metalimnion yield the most useful data.

2. *A comparison of sedimentation during stratification and overturn.* Table 17 summarizes the sedimentation of remains/cm²/day during stratification (Series 1 and W-2) and fall overturn (Series 2 and W-4). The increase in remains during overturn is quite striking. The greatest percentage increase in both years occurred in the lowermost vessel positioned about 1 m above the lake floor. The source of remains is suggested by examining the littoral-planktonic percentages in Table 18 between the lowermost vessels of the stratification and overturn series, and by comparing them to adjacent surface sediment. The nearest surface sediment examined in 1959 was 90 m away at station SS-1 and in 1961 in the immediate vicinity of the collector. At overturn in 1959 (Series 2) the littoral percentage declined, while the planktonic increased, and both were exceedingly close to those of nearby surface sediment (SS-1). This sug-

TABLE 17. A comparison of remains sedimented/cm²/day during stratification (Series 1 and W-2) and overturn (Series 2 and W-4) in 1959 and 1961.

Year	Depth (m)	Remains/cm ² /day		% increase
		Stratification	Overturn	
1959		<i>Series 1</i>	<i>Series 2</i>	
	9.8	3.3	---	---
	11.8	4.5	27.0	500
	13.8	4.4	32.6	642
1961		<i>Series W-2</i>	<i>Series W-4</i>	
	8.0	2.3	4.0	74
	11.0	--	4.9	---
	14.0	4.7	21.3	353

TABLE 18. Littoral-planktonic percentages during stratification and overturn in the lowermost collector vessels and in the nearest surface sediment (SS).

		Collector vessels		Surface sediment
		Stratification	Overturn	
Year				
1959		<i>Series 1</i>	<i>Series 2</i>	<i>SS-1</i>
	Littoral	52.7	33.8	34.0
	Planktonic	47.3	66.2	66.0
1960		<i>Series 3</i>		<i>SS-16</i>
	Littoral	58.2		24.9
	Planktonic	41.8		75.1
1961		<i>Series W-2</i>	<i>Series W-4</i>	<i>SS</i>
	Littoral	44.0	41.4	37.6
	Planktonic	56.0	58.6	62.4

gests that during overturn the primary source of remains is the neighboring surficial sediment that is brought into the circulating water column. The higher littoral percentage during stratification (Series 1) indicates a source having a higher littoral component, such as the littoral zone, but dilution by planktonic remains is likely since the remains traveled through open water.

In 1961 a comparable shift in the littoral-planktonic percentage after overturn was not found. The explanation must lie in the nature of sedimentation during Series W-2, since the percentages of Series W-4 and the surface sediment are similar. Quantitative plankton collections taken at the end of Series W-2 showed 200 *Daphnia*/liter, while at the beginning of Series W-4 only 1 *Daphnia*/liter was present. The high density during Series W-2 furnished a source of planktonic remains in the 14 m vessel whose *Daphnia* composition was 10% of the total remains—the highest percentage of *Daphnia* found in a deep collector vessel.

A littoral source of remains during stratification is again suggested by Series 3 of 1960. These percentages compare favorably with those of Series 1 in which a littoral origin of sediment is indicated.

This shift in composition is also seen by comparing the percentage of total remains, *Bosmina*, and *Sida* + chydorids per gram dry weight in the lowermost vessels of Series 2 (overturn) and Series 1 (stratification). Sedimentation of total remains increased 90% at overturn, but there was a 182% increase in *Bosmina* remains compared to only a 22% increase in *Sida* + chydorids, again indicating that deep-water sediment was circulating.

TABLE 19. Percentage chemical composition of sediment collected during stratification (Series 1) and overturn (Series 2) and of surface sediment at Station SS-1 in 1959. Depth of collectors and of water at SS-1 are in meters.

	Collector vessels					Surface sediment
	Stratification			Overturn		
	9.8	11.8	13.8	11.8	13.8	13.0
Organic content	18.0	19.7	20.2	15.1	10.9	10.9
CaCO ₃	45.5	37.6	36.8	29.8	33.1	33.1
Residue	36.5	42.7	43.0	55.1	56.0	56.0

A final study of sediment composition between stratification and overturn is shown in Table 19 in which the chemical analyses of Series 1 and 2 are compared to the nearby surface sediment at SS-1. There is a closer correspondence between overturn Series 2 and SS-1 than between SS-1 and Series 1, indicating that the sediment source for each series must be different. A lake floor source for Series 2 is indicated by its similarity to SS-1. These conclusions seem reasonable even after considering that conditions of sediment production are different in summer and fall, deriving partly from the increased turbulence and also the introduction of oxygen into the lower depths.

3. *Variations and similarities within a collector series during overturn.* If deep-water surface sediment was raised into the entire water column during fall overturn, then the sediment in all vessels should show certain similarities. On the other hand, a shallow-water contribution must be considered and also the height to which sediment is raised above the bottom. Various parameters of cladoceran remain analysis are presented in Table 20 for the vessels of overturn Series W-4 and the adjacent surface sediment. Numerous *C. sphaericus* had colonized the vessels at 3 m and undoubtedly contributed some exuviae, but otherwise the remains in all vessels are attributed to sedimentation. From the top to the bottom vessel of the series, there is an increase in the total remains/g sediment parameter. The best indication that surface sediment is raised into the water column is the similarity between the 14 m vessel and the surface sediment. The increase with depth in total remains/g, remains/cm², and cc/day is not surprising, since the water column over a vessel increases in length as depth increases. If surface sediment is raised to the 3 m vessel,

TABLE 20. Comparison of cladoceran remains in four collector vessels of overturn Series W-4 in 1961 and the adjacent surface sediment SS according to percentage composition, number of species represented, and number of remains per gram of various sediment parameters. Depths of collectors and of water at SS are in meters.

	Collector vessels				SS
	3.0	8.0	11.0	14.0	15.3
Littoral (%)	79.2	71.8	66.4	41.4	37.6
Planktonic (%)	20.8	28.2	33.6	58.6	62.4
<i>C. sphaericus</i> (%)	73.2	56.0	56.5	51.4	56.5
Other chydorids (%)	26.8	44.0	43.5	48.6	43.5
Chydorid species	6	14	17	18	15
Total species	9	20	22	24	22

Depth (m)	Total remains $\times 10^3/\text{g}$				
	Dry wt.	Organic	CaCO ₃	Residue	Inorganic
3.0	6.5	28.9	18.7	15.1	8.4
8.0	11.4	76.2	26.7	28.6	13.8
11.0	10.6	68.8	24.1	26.1	12.5
14.0	13.9	110.4	32.3	30.4	15.6
15.3 (SS)	14.1	106.7	31.6	33.0	16.3

a similarity in the proportion of remains might be expected in all collectors. This is not the case. The high proportion of littoral remains in the upper vessels indicates a shallow-water source for remains transported near the surface. Their sedimentation into the upper vessels masks any influence of material raised from deep-water sediment. Likewise, the sedimentation of remains from littoral areas into the lower vessels is not detectable due to the large quantity of sediment raised from the lake floor.

In summary, these sediment collector data amply show that the offshore displacement of littoral remains is not restricted to periods of overturn but also occurs during stratification. The time of greatest displacement is not known. Such information must come from epilimnetic vessels, but as these frequently became colonized by living Cladocera, they were unsuitable for such an analysis. The surface waters of a lake to a depth of at least several meters, corresponding to the epilimnion in summer, are in continual circulation during the ice-free period. Hence, under similar conditions of wind and turbulence the activity at the floor of the littoral zone and the transport of materials from there into the offshore surface waters should not differ appreciably between overturn and stratification. At overturn the deepwater sediment is carried into the circulating water and elevated slightly more than 1 m above the bottom. However, the similarity in composition between the sediment in the lowermost vessel at overturn and that of the nearby surface sediment suggests that the disturbed sediment tends to remain in the immediate vicinity and does not experience

a complete relocation at a single overturn. Rather the observed distribution of sedimentary remains is the resultant of a gradual offshore movement involving, probably, many periods of circulation.

Several suggested uses of cladoceran remains in collector studies that have emerged from this work will be briefly mentioned. The relative influence of inshore and deep-water sediment might be elucidated by extending a transect of collectors along the basin slope. This might also indicate the height to which sediment is raised during overturn. In an effort to mimic conditions at the mud-water interface, Kleerekoper (1952) used a low-sided vessel. Shifts in cladoceran composition could be approached by installing in such collectors some sediment foreign to the collector site. A subsequent analysis of the sediment after an appropriate period in the water might reveal the rate of turnover of the remains, especially if a means were devised to stain the chitin before placing the sediment in the collector.

The collector design shown in Figure 4 is highly recommended, but with the following modification. Attach the collector vessels to a cable connected to a horizontal cross bar secured to the top of the float. In this way, only the collector cable need be hauled to the surface. The anchor and float would stay in place.

DISCUSSION

The paleolimnologist in his attempt to draw interpretations from lacustrine sediments must usually limit himself to a single sedimentary column, and in almost every paleolimnological or paleoecological study the core is drawn from offshore sediment usually near the point of maximum depth. This was true for those analyses of fossil cladoceran remains mentioned in the Introduction. Recognizing that interpretations applicable to the entire lake have been drawn mainly from single cores or a single contemporary sediment analysis, the present study was undertaken to determine the validity of this procedure with respect to Cladocera. The location chosen must be representative of the lake's sedimentary cladoceran population and must faithfully reflect the inshore fauna, since substrate species of Chydoridae are abundantly preserved in the offshore sediments and are used for interpretive purposes. Furthermore, the offshore sediments are populated by remains contributed by plankters in the overlying water, and it is necessary to understand the integration of these two groups throughout the lake. An extension of these objectives is to determine the optimal sampling location when several or more lakes are to be compared on the basis of just a single sample from each. With these points in mind the surficial distribution was studied in three lakes of contrasting morphometry.

The distribution of chydorid species and their relative abundance are fairly uniform in the contemporary sediment of the three lakes studied, with similar results being obtained regardless of the sampling site. This is particularly useful when drawing up a species list or determining the percent composition of the chydorids. Often in deep-water sediments *Bosmina* remains so dilute the inshore representatives that examination is greatly extended. This could be remedied by sampling elsewhere, possibly upslope, knowing that the composition obtained from any location will be repre-

sentative of the entire lake. If the sample is taken from the littoral shelf the proportion of fragmented remains will be higher but this does not seem to change the percentage composition of species, suggesting that susceptibility to breakage is about equal among the remains of all species or is perhaps undetectable by the methods used. From the standpoint of the ratio of littoral and planktonic remains, a stabilization is usually found throughout the hypolimnion. There is a decreasing gradient of inshore remains, which continues into the upper hypolimnion. For this reason, in the present study, the percentage of littoral and planktonic remains used for comparison with the planktonic/littoral ratio was taken from deep-water sediment, for it was only in this region that the two components seemed to be stably and uniformly integrated.

Apparently a fairly good approximation can be obtained of the relative influence of inshore production by examining the proportion of littoral and planktonic cladoceran remains taken from the central plain, and as pointed out these data must be collected from deep-water sediment samples where downslope movement of inshore remains has ceased. This ratio bears a direct relationship to the relative area and volume of the littoral and planktonic zones, respectively, and should prove useful as an indicator of changing basin morphometry when comparing spectra in a single deep-water core. This seems to substantiate the original work of Brehm *et al.* (1948), who attempted to draw inferences regarding past basin morphometry from the proportion of chydorids and plankters.

This littoral-planktonic relationship was worked out on contemporary sediment taken from 10 lakes. Its usefulness depends on the discreteness of the two zones, but difficulties arise from *Chydorus sphaericus*, which frequently occurs as a plankter. Since the cosmopolitanism and habitat preferences of this species are little understood, it might be well to eliminate it when preparing data for this type of analysis.

The quantitative distribution of remains is not uniform over a lake floor, but the same major distributional patterns were evident in the three lakes studied here regardless of the basin slope. There was always some transitional feature in the upper hypolimnion shown either by a peak in the quantity of remains or by an interruption of a trend. Where then is the best sampling site when just one analysis is to reflect conditions in the entire lake? The central plain is favored, as the degree of change in cladoceran abundance from one location to another is minimal compared to other parts of the basin. This area offers certain advantages when comparing several lakes or spectra from the same lake. It is only near maximal basin depth that approximately uniform conditions are attained. Sediment resting on a slope can be transported downward, with instability increasing as a function of the slope angle. For example, in his shallow-water core from Lower Linsley Pond, Deevey (1942) found an unconformity suggesting that material had been removed from this section and redeposited in deeper water. Slopes on the central plain are negligible, and here gravitational transport must cease, since the ultimate repository for sediment has been reached. Frey (1960a) showed that the cladoceran population bears a definite relationship to the producing population by using a single deep-water surface sample from each of five lakes. His results might have been the same had he obtained sediment from comparable places, *e.g.*

near the upper hypolimnion or within the metalimnion, but had he collected at random throughout the lake it is doubtful that a correlation would have existed between cladoceran abundance and organic production because of the wide differences in cladoceran abundance along the basin slope. It is not surprising that in nine modern samples taken by Deevey (1942) in Linsley Pond, the quantitative abundance of *Bosmina* did not tend to vary consistently with increasing depth. Certainly, nine samples taken at random between comparable depths (6.4 to 14.5 m) in any of the three Indiana lakes studied here would show a similar inconsistency, since these depth limits would enclose the transitional region in the upper hypolimnion.

The sediment collector study has shown that during overturn surface deep-water sediment is raised at least 1 m into the water column. Tutin (1955) similarly found a mature sediment in her collecting vessels at overturn, and decided that at this time shallow-water deposits were being re-distributed. She followed *Asterionella* as an indicator of these dynamics. The results of Eggleton (1931) differ somewhat in that he found inshore debris in deep-water collectors following overturn, but he suggested that currents at this time might be sufficient to redistribute both littoral and profundal organisms. Perhaps the most informative paper on deep-water disturbances of sediment is that of Gorham (1958) who found 1 to 2-mm thick bands of green-colored algal colonies 5 to 10 mm beneath the mud surface, indicating a turbulent disturbance of the sediment—and this was prior to fall overturn. His evidence during autumn overturn strongly suggests that surface mud is elevated into the overlying water, since oxygen is present throughout the flocculent layer, and this degree of molecular oxygen diffusion is not possible in the short time involved. Alsterberg (1930, 1931) postulated that profile-bound density currents during both summer and winter stagnation can transport dissolved materials downslope, but he did not refer to their ability to transport particulate matter. Birge *et al.* (1928) and Hutchinson (1938) also consider density currents but only with respect to the transport of heat and solutions. Mortimer (1942) questions the existence of these currents by asking whether the small density increase produced in the water over the mud is sufficient to overcome the friction offered by the mud surface.

The studies of Bryson most directly approach the problem of sediment displacement. In a personal communication he agrees that deepwater sediments circulate during fall overturn, but the precise current velocity necessary for this disturbance is not known. He estimates that 30 cm/sec in Mendota would be sufficient and that this is not too high to occur in 20 m of water. Bryson further states the opinion that the strong surface and bottom currents and also the "stress-drop jet" currents (Bryson and Bunge, 1956) at the bottom of the epilimnion are sufficient to dislodge and transport sediment depending on the type of bottom.

Any disturbance of surface sediment during overturn to the extent that it completely alters the sediment composition does not occur. It was shown that events responsible for the quantitative distribution are occurring within the framework of thermal stratification, but the breakdown of stratification and the subsequent disturbance of the sediment does not erase the distributional patterns. In other words, even though the sediment is raised

into the overlying water at overturn, this disturbance does not induce a great displacement of the sediment that alters its composition at a particular place. This suggests that sediment elevated above the lake floor falls back again before extensive lateral displacement occurs. A corollary was seen in the sediment moved from the lake floor into the lowermost collecting vessels at overturn. The sediment in the vessels was of the same composition as that in the immediate vicinity of the collector. Compared to the flat lake floor at maximum depth, there was increased opportunity for this sediment to be moved elsewhere since the collectors were located on the basin slope and suspended sediment could have been moved by both lateral and downslope currents.

The surficial distribution of sedimentary cladoceran remains has been studied in three lakes of contrasting morphometry. In each type of analysis the results obtained for one lake were confirmed in the other two. Prior studies of fossil remains taken from deepwater cores appear to be valid based on the findings of this study. The optimal sampling location is the central plain of the basin. From one location to another in this region there is minimal variation in the distributional patterns, especially with respect to the number of remains per unit sediment weight. It is also in this area that the proportion of littoral and planktonic remains is stable. However, no advantages obtain by sampling in deep-water for compiling a species list or for determining the relative chydorid composition, since all sites appear to be equally reliable and in agreement with one another.

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Latitudinal Distribution of Chydorid Cladocera in the Mississippi Valley, Based on Their Remains in Surficial Lake Sediments¹

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ABSTRACT

This study was undertaken to define the latitudinal distribution of the Chydoridae in the Mississippi Valley by quantitative means. Data from 45 lakes covering an area from Lake Itasca, Minnesota, to New Orleans, Louisiana, were used. The remains the chydorids leave in lake sediments were identified and the relative abundance (percentage) of the remains of each species in each lake determined. *Chydorus sphaericus* was the single most abundant species in most lakes.

Regressions and correlation coefficients were computed for the most important species; however, *C. sphaericus* was eliminated from the total fauna so that more realistic values could be determined. Northern species were defined as those that either are restricted to the northern portion of the study area or show a statistically significant increase in abundance toward the north; southern species were defined as those that either are restricted to southern lakes or have a significant negative correlation with latitude; eurytopic species were defined as those that do not show a statistically significant correlation with latitude, occurring throughout the study area.

Of the 24 species whose distributions were analyzed statistically, 15 were chosen to form indicator groups. Eurytopic species were: *Alona rectangula*, *Camptocercus rectirostris*, *Chydorus globosus*, *Leydigia leydigi*, and *Pleuroxus denticulatus*. Northern species were: *Acroperus harpae*, *Alona quadrangularis*, *Alonella excisa*, *Eurycercus lamellatus*, and *Graptoleberis testudinaria*. Southern species were: *Alona karua*, *Alonella hamulata*, *Chydorus* spp., *Euryalona occidentalis*, and *Leydigia acanthocercoides*.

As expected from the definitions of the indicator groups, northern species dominated in the north and southern species in the south. However, along the middle portion of the latitudinal transect eurytopic species were dominant in most lakes.

Regressions of the percent of northern and southern indicator species against latitude crossed near the median latitude of the transect (38.50°N). The 95% confidence limits of these two regressions defined a Zone of Statistical Overlap between 35.80°N and 39.25°N, in which the eurytopic indicator species reached their peak of abundance. North of this zone is a Northern Zone, characterized by dominance of northern species. South of the Zone of Statistical Overlap a Transition Zone was defined, extending south to 31.75°N, which was characterized by a decreasing dominance of eurytopic forms and a gradual increase in the relative abundance of southern forms. In the Southern Zone south of 31.75°N southern species were clearly dominant.

The Zone of Statistical Overlap is coincident with the region in which lakes may be either dimictic or warm monomictic, depending on the severity of the winter. The summer temperatures in the Zone of Statistical Overlap appear to be those necessary from the viewpoint of climate to form a barrier for the colonization southward of strictly northern species and at the same time are not sufficiently high to permit large populations of southern chydorids to build up consistently year after year. Hence, the eurytopic forms are able to gain ascendancy in this zone.

The chydorids appear to be excellent indicators of macro-climatic conditions. The chydorid spectrum of a particular lake indicates general climatic conditions and general thermal regimes of the lake. The importance of these findings to paleolimnology and Pleistocene ecology are briefly discussed.

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INTRODUCTION

Previous biogeographical studies of the Cladocera have depended upon collections being made from the living populations (e.g. Richard, 1894; Brehm, 1933). In addition there have been studies involving altitude as a factor influencing cladoceran distribution (Carl, 1940; Dodds, 1919, 1920; Reed and Olive, 1958). The populations fluctuate rapidly in size as well as species composition not only over short periods of time but also from year to year. Therefore attempts to work out the biogeography of the Cladocera must depend on long and intensive collecting. However, collecting even at very short intervals does not result in accurate analysis of the abundance of species relative to the total population.

These difficulties can be obviated by studying the remains that the chydorids leave in lake sediments. In 1958 Frey showed that the cladoceran family, Chydoridae, leaves recognizable remains in lake sediments. Further work (Frey, 1959) showed that the chydorids possess head pores which are of taxonomic and phylogenetic importance. This was followed by a paper (Frey, 1960) showing that a single off-shore sediment sample could yield a species list of nearly all the chydorid species that have lived in the lake over the period of time represented by the sediment sample. In this and a subsequent paper (1961) Frey suggested that this approach could be used in studying the biogeography of the family. The present study is the first attempt to study the biogeography of the Chydoridae quantitatively.

In 1918 Birge stated that the cladoceran faunas of various regions were on the whole strikingly similar, but with some forms peculiar to each region. Writing in the new edition of *Fresh-Water Biology* (1959), Brooks states that the Cladocera are sometimes cited as a group in which studies of geographical distribution promise little of interest because species are distributed so widely. However, a significant number of species are restricted to parts of a single continent, from which Brooks concluded that careful studies of taxonomy and distribution should yield data of considerable zoogeographic interest.

The chydorid fauna of the northern Mississippi Valley is quite well known, mainly through the efforts of Birge. Some of these species are definitely northern in their distributions. The southern portion is not so well known, but already in 1918 Birge was able to cite certain species that

had southern affinities. This suggests that the chydorids might exhibit three main groups of species: a northern, a southern, and a cosmopolitan group. This study was undertaken to ascertain whether the three major species groupings actually exist, and if so where the northern and southern faunas meet and to what extent they overlap. Suggestions might also be forthcoming on factors that keep the two regional groups discrete.

The Mississippi Valley was chosen for this study because it presents an ideal region for biogeographical study of freshwater biota. Thousands of lakes exist in the glaciated portion of the Valley, and several hundred oxbow lakes line the southern reaches. The Valley is a major flyway for migrating birds, and hence there could be a constant introduction of species via resting eggs from both directions.

Dispersal of the Cladocera in general is facilitated by the production of resistant eggs, sexually produced, which can be easily transported by various means, the most often mentioned being birds and the wind. With such a high rate of passive dispersal any species that could live in a given lake would be constantly introduced. The Mississippi Valley thus assumes the character of a fluid distributional situation. Species can quickly colonize habitats previously unfavorable to them, and a rapid response to broad changes in climate can be expected. In addition, the species spectrum in a lake can change in response to ecological conditions in specific habitats. It has already been suggested by Frey (1959) that this rapid colonization by micro aquatic organisms makes them more valuable than terrestrial plants as indicators of climatic change as well as of associated changes in the trophic level of a lake.

The assumptions on which this study is based are: 1) all species of the Chydoridae leave remains in lake sediments; 2) there is no differential destruction of remains, and hence the micro-fossil populations are a direct reflection of the living populations that produced them; 3) each living chydorid produces approximately the same number of exuviae, which become incorporated in the sediments. Mueller (1964) has already shown that the relative proportion of chydorid species to one another remains constant over the entire lake bottom. Hence, for studies of the kind reported here a sediment sample from anywhere in the lake is adequate.

The findings of this study, in addition to their zoogeographical importance, also shed light on the climatic agents that seem to be important in controlling the changing chydorid fauna in a north-south transect of the Mississippi Valley. Eventually lists of species might be drawn up that indicate the climatic conditions under which these different groupings of species thrive.

METHODS

A total of 56 lakes was sampled during the course of the study, but data on only 45 are reported here. They were selected at random, although in the southern portion of the Valley only oxbows were selected that were located inside the levee system. The lakes of northern Indiana, Wisconsin, and Minnesota are glacial in origin, whereas the lakes along the lower Mississippi Valley are either oxbows or artificial. The study covered the entire length of the Valley from Lake Itasca, Minnesota, to New Orleans, Louisiana.

The lakes were sampled during two successive years, comprising two trips to New Orleans, one to northern Minnesota, and one to the Indiana Lake District. Each lake was visited only once. Samples of offshore surface sediments were taken with a 6" x 6" Ekman dredge from a boat, and no attempt was made to find the deepest portion of the basin.

Water samples were collected at the surface of the lake by directly filling two polyethylene bottles. One sample was brought back to the laboratory for use in measuring specific conductivity, color, and total dissolved solids. The other sample was used for measuring pH and alkalinity in the field. Hydrogen-ion concentration was measured using a Beckman Model N meter. Alkalinity was determined by titrating the sample to pH 4.4 with N/44 H₂SO₄ using the pH meter as an indicator of pH change.

Dissolved color as ppm of potassium chloroplatinate was measured by means of a U.S.G.S. standard color set. Total dissolved solids were determined gravimetrically on a filtered 500-ml aliquot of water, which had been slowly evaporated in a tared crucible placed in a sand bath. This residue was ashed at 550°C in a muffle furnace, the loss on ignition resulting from one hour's ashing being an approximation of the total dissolved organic matter. Conductivity was measured with a Model RC 16 conductivity bridge manufactured by Industrial Instruments, Inc. Resistances as measured by the instrument were converted to micromhos at 20°C.

The water was poured off the sediment samples, and the sediment was thoroughly mixed in a bucket. A 500-ml jar was filled with the material which in all cases was more than sufficient for the analyses.

Sediment parameters were determined on a given volume of mud, which was placed in a tared crucible and dried 24 hours in an oven at 95°C. Dry weight was determined, and the sample was then ashed for one hour at 550°C in a muffle furnace. The loss on ignition was measured, and the sample was reheated in the furnace at 950°C for 3 hours. Thus inorganic matter minus any CaCO₃ present was measured. Presence of CaCO₃ was determined by flooding a portion of sediment with 10% HCl and examining for effervescence under a low power microscope. In non-clacareous sediments a loss at 950°C of up to 3% dry weight was recorded. This was interpreted as water bound in clay minerals and was not calculated as CaCO₃. Carbonate content was calculated only for sediments showing a positive reaction to acid treatment.

A known volume of sediment (up to 50 cc) was prepared for examination of cladoceran remains by elimination of carbonate, if present, by treatment with 10% HCl on a magnetic stirrer hotplate for approximately 1½ hour. The resulting suspension was centrifuged, and the excess water and acid pipetted off. The sediment was then resuspended in 10% KOH, heated, and stirred for one hour, after which the sediment was passed through a fine-mesh screen of 250 meshes per inch (ca. 50 microns) which was soldered to a metal cup. This cup was placed in a pyrex pan on the magnetic stirrer and a large volume of distilled water washed through it, which removed silt and clay particles. Sand grains, cladoceran remains, and plant fragments remained in the cup. This suspension was centrifuged to reduce it to a manageable volume and preserved in formalin. A measured volume (0.05 ml) of the preserved suspension was mounted on a slide in

a drop of glycerine jelly stained with gentian violet and covered with a 22-mm cover slip. Cladoceran remains were counted at 100X by systematically examining the entire slide with a mechanical stage. At least 200 remains of chydorids which were recognizable to species were counted in most samples.

Various sources were used in identification of the remains, including Brooks (1959), Lilljeborg (1900), and Frey (1958, 1959, 1960, 1961). In addition, remains were compared with reference material in the collection of D. G. Frey and also with living specimens collected by the author.

DESCRIPTION OF LAKES

The 11 lakes of the 56 that are not reported on here proved to have insufficient chydorid remains in their sediments for the present study. Of these 11 lakes 6 were artificial lakes (man-made impoundments), and reasons for the sparsity of remains will be discussed below.

Table 1 lists the lakes used in the study with their locations, type, and some characteristics of their waters at the time of sampling. Table 2 shows the proximate sediment analyses for the lakes. In both tables the lakes are arranged in a north-south sequence regardless of longitude.

The mean total dissolved solids (TDS) was 158.4 mg/L, and as would be expected there is no significant correlation between TDS and latitude ($r = 0.133$, 42 d.f.). However, the percent dissolved organic matter in the TDS increases significantly towards the south ($r = -0.435^{**}$, 42 d.f.).

The mean dissolved organic matter was 44.3 mg/L. This is higher than values reported by Birge and Juday (1926a, 1926b, 1927, 1934). Their values were derived by calculation from analyses of organic N and C in centrifuged water samples. The mean dissolved organic content of 12 lakes in southern Wisconsin was 14.28 mg/L, and of 84 more oligotrophic lakes in northeastern Wisconsin 12.8 mg/L. In their final report (1934) they give the results from 529 lakes in NE Wisconsin. The mean TDS was 43 mg/L, compared to a mean of 200 mg/L in the lakes of southern Wisconsin. The mean total organic matter in the northern lakes was 16-17 mg/L, of which 8-9% was planktonic.

In order to determine if the differences between my data and those of Birge and Juday are real or if they are a function of the two methods used, a comparison was made between the TDS and specific conductivity ($K_{20} \times 10^{-6}$). The regression of the data in this study is shown as *A* in Figure 1. It should be noticed that the regression does not go through the origin of the coordinates but intercepts the Y-axis at 37.2. Also plotted in Figure 1 is the theoretical regression *B* calculated from data presented by Rodhe (1949, 1951). This line passes close to the origin of the coordinates. The third regression *C* in Figure 1 represents only the dissolved inorganic solids in the present study. These data were calculated by subtracting the amounts of dissolved organic matter from the TDS, the resultant being dissolved inorganic salts. This regression falls quite close to the theoretical one calculated from Rodhe's data. It can therefore be concluded that in regression *A* the magnitude of displacement on the Y-axis is an approximation of the mean dissolved organic matter. Interionic attraction in solution,

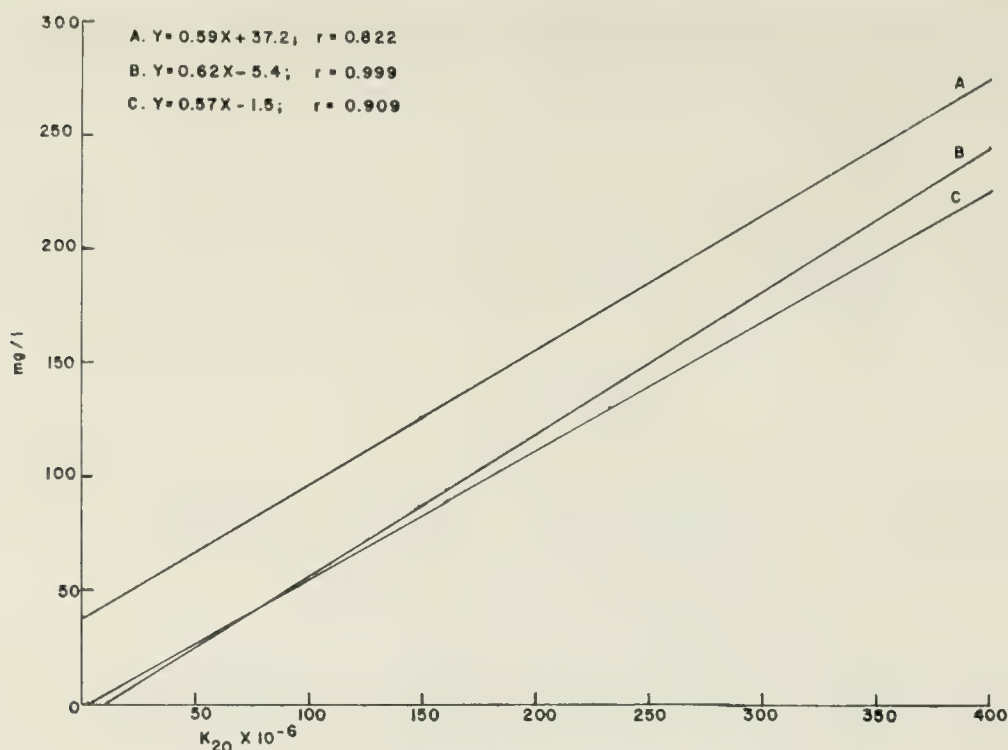


FIG. 1. Specific conductivity *vs* dissolved solids. Regression A is based on the TDS data in this study *vs* conductivity. Regression B is based on the theoretical data of Rodhe. Regression C is the TDS of this study minus loss on ignition, thus representing only the inorganic salts.

as is well-known to physical chemistry and is mentioned by Rodhe, could account for some of the difference between 37.2 and 44.3 mg/L.

The method used here was similar to the one outlined in Standard Methods of Water Analysis (A.P.H.A., 1955), which is recommended by Hutchinson (1957). The method used by Birge and Juday is no longer recommended. The differences between the values for dissolved organic matter reported here and those of Birge and Juday are probably due to methodology.

Relative amounts of organic matter in the sediment also show a significant correlation with latitude ($r = 0.756^{**}$, 43 d.f.), which is direct rather than inverse as for dissolved organic matter. In addition sedimentary dry weight increases significantly southward ($r = -0.465^{**}$, 43 d.f.). These two correlations, opposite to each other, can be explained on the basis of increased rates of sedimentation in southern lakes. All of the oxbows and a large number of the artificial lakes in this study are located in the South (Table 1). Both these lake types have in common the fact that they are subjected to tremendous deposition of silt and clay. Artificial lakes, being impounded streams, cause a decrease in bed load of the stream, with the resulting high rate of deposition. Oxbow lakes receive a great amount of run-off from very flat, silty floodplains that are under cultivation, which accounts for their high rate of sedimentation. If one assumes a greater compaction and greater density of clastic sediments, this could account for the higher dry weight of sediments in the South. In addition the greater sedimentation rate of clastics would dilute

TABLE 1. Lakes, locations, and some characteristics of their waters, arranged in order of decreasing latitude.

No., lake, state	Lat.	Long.	Type ¹	pH	Acid combining capacity me/L	Dissolved color ppm	K ₂ O × 10 ⁻⁵	TDS mg/L	% loss on ignition	Collected		Surface temp. °C
										Month	Year	
1. Itasca, Minn.	47.08	95.25	N	7.5	3.66	10	305	184.4	28.8	V	61	11.8
2. Big Pelican, Minn.	46.58	94.17	N	7.6	2.46	5	201	132.6	25.4	V	61	13.8
3. Ruth, Minn.	46.42	94.25	N	7.5	1.70	10	128	83.2	17.8	V	61	12.2
4. Little Rock, Minn.	45.75	94.17	N	7.7	2.48	20	226	148.2	17.3	V	61	11.4
5. Briggs, Minn.	45.50	93.92	N	8.2	2.64	5	216	138.4	20.6	V	61	11.8
6. Big, Minn.	45.33	93.75	N	8.2	3.42	5	287	196.0	37.0	V	61	11.5
7. White Clay, Wisc.	44.84	88.25	N	—	—	—	430	—	—	—	—	—
8. James, Ind.	41.58	85.08	N	6.8	2.32	5	329	240.2	25.8	IV	61	—
9. Crooked, Ind.	41.58	85.00	N	6.7	2.22	10	268	193.0	23.6	IV	61	—
10. Pleasant, Ind.	41.50	85.00	N	6.7	2.04	5	303	156.4	27.4	IV	61	—
11. Hamilton, Ind.	41.50	84.92	N	7.1	2.41	20	293	218.8	28.8	IV	61	—
12. Chapman, Ind.	41.25	85.75	N	6.8	2.72	20	320	232.0	18.5	IV	61	—
13. Storey, Ill.	41.00	90.40	A	8.0	3.50	10	349	259.4	18.9	V	61	16.0
14. Springfield, Ill.	39.75	89.58	A	7.6	2.50	10	325	225.6	22.2	V	61	16.1
15. Lenape, Ind.	39.17	87.08	A	6.7	1.21	20	209	153.4	22.4	V	61	—
16. Shakamak, Ind.	39.17	87.08	A	6.9	1.39	10	210	155.0	14.9	V	61	—
17. Starve Hollow, Ind.	38.84	86.08	A	7.3	0.76	40	108	90.8	22.0	III	61	—
18. Horseshoe, Mad., Ill. ²	38.75	89.82	O	8.3	1.93	40	407	288.8	18.6	X	61	8.9
19. Geneva, Ind.	38.75	85.00	A	7.1	1.07	20	142	106.6	15.9	III	61	—
20. Carbon, Ill.	37.75	89.33	A	7.8	2.14	20	212	147.2	23.1	X	61	16.3
21. Little Grassy, Ill.	37.58	89.17	A	7.2	0.46	10	66	41.2	12.1	X	61	18.0
22. Otter Pond, Ill.	37.50	89.40	N	6.5	1.31	40	102	85.8	37.8	X	61	—
23. Horseshoe, Ill. ²	37.17	89.25	O	7.8	0.83	40	116	119.8	50.9	VI	60	27.9
24. Reelfoot, Tenn.	36.33	89.25	N	7.4	2.54	65	182	140.8	38.6	VI	60	24.0
25. Stave, Ark.	35.42	90.17	O	7.7	1.51	40	158	137.8	89.4	X	61	—
26. Horseshoe, Ark.	34.92	90.33	O	8.1	2.04	10	158	119.2	27.6	VI	60	29.6
27. Annette, Miss.	33.50	91.00	A	9.5	3.04	35	164	150.2	46.2	VI	60	30.9
28. Alligator, Miss.	33.25	90.84	N	7.6	4.85	90	503	367.2	7.8	VI	61	27.0
29. Washington, Miss.	33.17	91.08	O	8.5	2.13	110	177	140.4	38.7	VI	60	30.5
30. Providence, La.	32.84	91.25	O	8.3	2.48	5	191	172.2	36.9	VI	60	28.5
31. St. Joseph, La.	32.08	91.25	O	8.3	2.30	50	184	270.4	35.8	VI	60	32.3
32. Bruin, La.	32.00	91.25	O	8.6	1.91	5	153	281.0	23.7	VI	60	29.9
33. St. John, La.	31.75	91.70	O	8.2	1.07	25	202	166.0	30.9	VI	60	27.5
34. Cane River, La.	31.75	93.17	A	7.8	4.22	90	404	306.8	28.6	VI	60	31.0
35. Concordia, La.	31.66	91.50	O	8.8	2.66	10	230	196.8	40.0	VI	60	31.2
36. Horseshoe, La.	31.50	91.75	O	8.5	1.26	40	219	132.6	27.8	VI	61	28.9
37. Bennet's, La.	30.92	92.50	N-A	6.4	0.45	90	53	75.8	31.4	VI	60	27.5
38. Miller's, La.	30.75	92.33	N-A	6.8	0.59	50	59	70.4	77.7	VI	60	28.0
39. Chicot, La.	30.75	92.25	N-A	9.0	0.36	20	36	46.2	54.4	VI	60	29.7
40. Cannon's, La.	30.75	91.58	A	8.8	2.36	40	196	139.6	37.4	VI	60	31.8
41. Cazan's, La.	30.75	92.25	N-A	7.1	0.83	25	83	60.8	46.4	VI	60	—
42. False River, La.	30.66	91.50	O	6.4	1.18	15	222	167.8	34.6	VI	60	28.5
43. Dun-Roamin, La.	30.50	92.50	A	6.3	0.73	10	93	66.0	21.8	VI	61	29.2
44. Lake Vue, La.	30.50	92.50	A	8.2	0.52	5	92	53.2	38.0	VI	61	32.7
45. Audubon, La.	29.92	90.17	A	6.7	1.41	25	165	117.0	28.9	VI	61	27.9

1A - Artificial Lakes (Hutchinson, Type 73) ; O - Oxbow Lakes (Hutchinson, Type 55) ; N - natural lakes, except oxbows; the lakes in Minnesota, Wisconsin, and northern Indiana are glacial lakes; Reelfoot Lake, Tenn. was formed by the New Madrid earthquake in 1811; NA - Natural Lake which has been enlarged by the addition of a dam.

²There were 4 Horseshoe Lakes used in this study. Two of these are in Illinois. Horseshoe, Mad., Ill. refers to a lake at Madison, Ill. The other lake of this name in Illinois, which is simply referred to as Horseshoe, Ill., is located near the confluence of the Ohio and Mississippi Rivers, just north of Cairo, Ill.

TABLE 2. Sediment analyses of lake samples.

No., lake, state	Dry wt. mg/cc	Ash wt. (550°C) mg/cc	% loss on igni- tion (550°C)	Residue ¹ mg/cc	% CaCO ₃
1. Itasca, Minn.	146.9	121.1	18.5	19.2	69.5
2. Big Pelican, Minn.	114.1	86.6	24.1	17.1	61.0
3. Ruth, Minn.	45.3	25.2	44.4	24.4	---
4. Little Rock, Minn.	119.2	78.2	34.3	74.9	---
5. Brigg's, Minn.	138.2	104.9	24.0	64.0	29.6
6. Big, Minn.	99.8	75.7	24.2	51.6	24.2
7. White Clay, Wisc.	132.8	98.1	25.7	61.0	27.9
8. James, Ind.	284.5	251.6	11.6	82.6	59.4
9. Crooked, Ind.	130.0	101.0	22.3	62.4	29.8
10. Pleasant, Ind.	97.1	67.4	30.5	40.2	28.0
11. Hamilton, Ind.	52.6	34.7	34.0	43.5	17.3
12. Chapman, Ind.	216.6	185.2	14.5	123.4	28.6
13. Storey, Ill.	682.4	650.1	4.8	638.3	---
14. Springfield, Ill.	456.2	424.2	7.1	415.2	---
15. Lenape, Ind.	305.7	278.4	8.9	274.1	---
16. Shakamak, Ind.	294.4	265.8	9.7	262.1	---
17. Starve Hollow, Ind.	443.3	413.6	6.7	406.0	---
18. Horseshoe, Mad., Ill.	294.1	254.0	13.7	220.5	11.4
19. Geneva, Ind.	739.2	700.4	5.3	695.0	---
20. Carbon, Ill.	419.8	388.5	7.5	384.8	---
21. Little Grassy, Ill.	427.8	400.8	6.4	395.1	---
22. Otter Pond, Ill.	334.2	288.3	13.7	255.8	9.7
23. Horseshoe, Ill.	152.9	121.4	20.5	115.7	---
24. Reelfoot, Tenn.	158.9	136.9	13.8	134.0	---
25. Stave, Ark.	182.7	159.3	12.9	156.5	---
26. Horseshoe, Ark.	257.2	230.7	10.3	226.3	---
27. Annette, Miss.	297.6	266.8	10.4	261.2	---
28. Alligator, Miss.	117.9	99.4	15.7	93.7	---
29. Washington, Miss.	209.7	186.3	11.4	179.3	---
30. Providence, La.	532.8	503.5	5.5	497.9	---
31. St. Joseph, La.	145.6	123.9	14.9	120.6	---
32. Bruin, La.	266.1	242.7	8.9	237.4	---
33. St. John, La.	376.3	350.5	7.4	345.0	---
34. Cane River, La.	348.2	317.4	8.9	309.8	---
35. Concordia, La.	221.2	196.4	15.8	193.3	---
36. Horseshoe, La.	219.2	196.7	10.3	192.0	---
37. Bennet's, La.	143.4	117.0	18.1	113.0	---
38. Miller's, La.	478.8	456.4	6.1	454.1	---
39. Chicot's, La.	124.6	101.1	18.8	98.6	---
40. Cannon's, La.	212.9	184.7	13.3	180.5	---
41. Cazan's, La.	521.8	490.2	6.1	479.9	---
42. False River, La.	407.8	380.0	6.8	374.4	---
43. Dun-Roamin, La.	374.8	345.5	7.3	342.3	---
44. Lake Vue, La.	376.7	347.5	7.8	345.1	---
45. Audubon, La.	239.8	214.1	10.8	207.1	---

¹ Residue = inorganic minus any CaCO₃ present, as in Frey (1960). Where no carbonate is present the discrepancy between weight of residue and ash weight was interpreted as water of hydration.

TABLE 3. Lakes whose sediments did not yield enough chydorid remains for use in this study.

Lake	Lat.	Long.	Type ¹	Dry wt. mg/cc	Ash wt. (550°C) mg/cc	% loss on ignition (550°C)
Hovey, Ind.	37.84	87.92	N	482.9	438.5	9.2
Grand Tower, Ill.	37.58	89.50	A	427.2	399.3	7.8
Big, Ark.	35.84	90.17	N	371.6	337.7	9.1
Johnson's, Tenn.	35.75	89.84	N	388.4	354.9	8.6
Sardis, Miss.	34.50	89.75	A			
Grenada, Miss.	33.75	89.66	A			
Beulah, Miss.	33.75	91.00	N	362.2	331.2	8.6
Iatt, La.	31.66	92.75	A			6.5
Old River, La.	31.58	91.50	N	382.6	347.8	9.1
Charles, La.	30.25	93.25	N-A	534.1	504.2	5.6
Arthur, La.	30.08	92.66	N-A	467.3	423.5	9.4
Mean				427.0		8.2

¹ For explanation of types, see Table 1.

the relative amounts of organic sediments, thereby resulting in a greater percentage of organic sediment in northern glacial lakes.

As stated previously, 11 lakes did not have sufficient chydorid remains in their sediments for the purposes of the present study. They comprise 6 artificial lakes and 5 natural lakes (Table 3). For the 8 lakes for which sediment analyses are available the mean dry weight was 427.0 mg/cm³ compared to 274.2 mg/cm³ in the other 45 lakes listed in Table 2. Three lakes had sediments so gritty and coarse that it was not feasible to make a volumetric measurement of the mud. For this reason only an approximation of the percent loss at 550°C is available for Lake Iatt. Lakes Sardis and Grenada, Mississippi, both impoundments, had sediments that to all appearances seemed to be merely wet clay that had been washed in from the watershed. Practically no cladoceran remains were present in these sediments. Lake Charles, Louisiana, had a TDS value of 2182.8 mg/L, indicating a brackish water situation. Crabs now live in the lake. Few cladoceran remains were found in the sediments, as would be expected since the chydorid Cladocera are confined almost entirely to fresh water.

With the exception of Big Lake, Arkansas, all the natural lakes in Table 3 are oxbows, which are flooded by the river in spring. The resulting deposition dilutes whatever chydorid remains were deposited during the previous year.

It can be concluded that in lakes with excessively high rates of clastic deposition, especially such as new impoundments, the chydorid remains are so diluted by allochthonous material that study of them is not feasible or at least is difficult.

RESULTS

Table 4 gives for each lake the list of chydorids recovered and the percentage composition of the total microfossil population. In each case "unknowns" were included in the total percentage, although "unrecognizables" were not. The distinction between these two groups is that unknowns

TABLE 4. Chydorid species found in each lake, and percentage composition of local faunas. Unknowns are included in the total fauna, unrecognizables are not.

No. lake, state	Number of species	<i>Euryceus lamellatus</i>	<i>Camptocercus rectirostris</i>	<i>Camptocercus oklahomensis</i>	<i>Acroporus harpae</i>	<i>Graptolchebis testudinaria</i>	<i>Alona affinis</i>	<i>Alona quadrangularis</i>	<i>Alona rectangularis</i>	<i>Alona guttata</i>	<i>Alona costata</i>	<i>Alona karua</i>	<i>Alona monacantha</i>	<i>Alona intermedia</i>
1. Itasca, Minn.	19	3.9	0.3	---	1.6	0.3	2.9	7.4	4.2	0.6	0.3	---	---	---
2. Big Pelican, Minn.	21	3.4	4.3	---	8.0	2.8	3.7	2.8	3.7	---	---	---	---	---
3. Ruth, Minn.	16	0.6	0.7	---	0.7	1.0	2.1	4.1	1.0	1.0	---	---	---	---
4. Little Rock, Minn.	19	1.2	2.9	---	0.3	1.4	0.8	1.5	2.3	0.3	---	---	---	---
5. Brigg's, Minn.	13	3.2	2.5	---	4.8	---	0.2	0.9	0.2	---	---	---	---	---
6. Big, Minn.	16	1.8	1.3	---	5.5	0.5	2.3	3.8	1.0	---	---	---	---	---
7. White Clay, Wis.	19	1.5	3.0	---	7.1	2.1	7.4	4.0	3.8	0.6	---	---	---	---
8. James, Ind.	21	6.1	2.2	---	15.6	3.5	1.3	10.8	1.7	0.4	---	---	---	---
9. Crooked, Ind.	16	4.8	---	---	9.3	3.3	5.6	1.5	2.2	0.4	---	---	---	---
10. Pleasant, Ind.	16	1.9	0.5	---	6.5	4.7	0.9	2.8	3.3	2.3	0.5	---	---	---
11. Hamilton, Ind.	16	4.1	1.0	---	1.7	3.1	1.0	1.7	3.4	---	---	---	---	---
12. Chapman, Ind.	18	1.9	2.3	---	5.3	6.5	2.3	3.1	3.1	---	0.4	---	---	---
13. Storey, Ill.	11	0.2	0.2	---	---	---	0.5	---	4.7	---	---	---	---	---
14. Springfield, Ill.	11	---	0.5	---	---	0.5	---	---	8.5	---	---	---	---	---
15. Lenape, Ind.	12	---	2.8	---	---	2.8	2.0	---	3.6	---	---	0.4	---	---
16. Shakamak, Ind.	15	0.5	1.8	---	---	0.9	0.5	1.6	8.3	0.5	---	1.4	---	---
17. Starve Hollow, Ind.	14	2.6	0.8	---	0.4	1.1	1.1	---	2.3	---	---	---	---	---
18. Horseshoe, Mad., Ill.	11	---	---	---	---	---	1.1	4.6	4.3	---	---	0.4	---	---
19. Geneva, Ind.	8	---	---	---	---	---	2.0	0.5	1.5	---	---	---	---	---
20. Carbon, Ill.	9	---	---	---	---	---	---	2.2	5.5	---	---	---	---	---
21. Little Grassy, Ill.	15	---	1.4	---	---	---	0.9	7.5	3.3	0.5	0.5	---	---	---
22. Otter Pond, Ill.	17	4.2	5.4	---	---	1.3	0.8	0.4	---	---	---	29.7	---	---
23. Horseshoe, Ill.	18	2.5	1.5	---	---	---	2.0	2.0	1.0	---	---	5.0	---	---
24. Reelfoot, Tenn.	13	1.9	1.4	---	---	---	1.0	5.8	10.6	---	---	1.0	---	---
25. Stave, Ark.	13	---	---	---	---	---	---	2.7	1.3	---	---	6.4	---	---
26. Horseshoe, Ark.	18	1.0	3.1	---	---	---	1.0	5.4	3.6	---	---	4.3	0.3	---
27. Annette, Miss.	11	---	---	---	---	---	1.5	2.8	1.8	---	---	---	---	---
28. Alligator, Miss.	28	---	1.5	---	---	---	0.4	---	4.1	---	---	3.0	1.1	---
29. Washington, Miss.	10	---	5.3	---	---	---	---	3.9	6.3	---	---	---	---	---
30. Providence, La.	10	---	2.1	---	---	---	1.3	3.3	5.5	---	---	---	---	---
31. St. Joseph, La.	15	---	7.9	---	---	---	---	1.2	3.3	---	---	2.5	---	---
32. Bruin, La.	17	---	6.1	---	---	---	1.9	4.5	4.9	---	---	2.3	---	---
33. St. John, La.	12	---	5.2	---	---	---	---	3.8	7.0	---	---	---	---	---
34. Cane River, La.	14	---	3.4	0.5	---	---	---	---	0.5	---	---	2.4	---	---
35. Concordia, La.	18	---	6.4	---	---	---	0.3	2.8	0.6	---	---	0.6	---	---
36. Horseshoe, La.	14	0.5	1.0	---	---	---	0.5	1.0	5.3	---	---	---	---	---
37. Bennet's, La.	18	1.2	0.4	---	0.4	---	0.4	0.4	1.2	---	---	2.9	---	0.8
38. Miller's, La.	18	6.6	11.0	1.1	---	---	9.6	3.4	1.1	---	0.3	11.5	---	---
39. Chicot, La.	21	1.6	3.5	---	---	---	0.3	0.3	---	0.5	---	16.9	---	---
40. Cannon's, La.	14	---	1.8	---	---	---	0.2	---	---	---	---	20.2	---	---
41. Cazan's, La.	16	9.7	1.9	---	---	---	---	---	1.9	0.5	---	18.5	5.5	---
42. False River, La.	15	---	12.9	0.4	---	---	---	0.4	0.7	---	---	2.9	---	---
43. Dun-Roamin, La.	16	---	2.3	0.8	---	---	0.8	2.7	2.7	0.8	---	0.4	---	---
44. Lake Vue, La.	12	---	0.4	---	---	---	0.2	0.2	0.2	---	---	0.2	---	---
45. Audubon, La.	12	---	1.5	---	---	---	---	0.8	0.4	---	---	0.4	---	---
No. of occurrences	--	24	39	4	14	16	36	37	42	12	6	22	3	1
Mean abundance where found	---	2.8	2.9	0.7	4.8	2.2	1.4	2.9	2.3	0.7	3.3	6.0	2.3	0.8

are those remains that are recognizable as chydorids but cannot be assigned to any species because of our still incomplete knowledge of isolated skeletal components. Unrecognizables are fragments that in all probability could be identified if they were not so fragmented or distorted in mounting. These occurred very seldom and were mostly fragments of head shields or shells. The number of unrecognizables is a good criterion of the degree of fragmentation of remains in a particular lake.

	<i>Alona verrucosa</i>	small <i>Alona</i>	<i>Pleuroxus</i> <i>trigonellus</i>	<i>Pleuroxus</i> <i>denticulatus</i>	<i>Pleuroxus</i> sp.	<i>Pleuroxus procurtus</i>	<i>Pleuroxus aduncus</i>	<i>Pleuroxus hastatus</i>	<i>Kurcia latissima</i>	<i>Chydorus sphaericus</i>	<i>Chydorus faviformis</i>	<i>Chydorus globosus</i>	<i>Chydorus</i> spp.	<i>Alonella nana</i>	<i>Alonella excisa</i>	<i>Alonella exigua</i>	<i>Alonella acutirostris</i>	<i>Alonella rostrata</i>
	3.2	0.6	1.0	0.3					0.3	66.0	0.6	0.6		2.3	1.6	0.3		
	6.4	0.9	2.4	1.8	0.6				1.8	40.1	2.1	0.9	0.3	4.9	7.0	0.6		
	3.1		0.6	0.1	0.1					80.9					0.9	0.3	0.3	
	1.8		0.4	0.3	0.1		0.1		0.3	82.4		0.3			0.8			
	0.7		1.4		0.5					82.7	0.2				0.5	0.2		
	1.5	0.2	1.5	0.2	0.2				1.3	76.2		0.2		0.2	1.0			
	8.9	0.6	1.2	2.4					0.9	44.5	0.9	0.6		5.3	3.3			
	9.5	0.4	0.4	0.9	1.7				0.9	23.5	2.2	1.7		3.5	5.6	2.6	0.4	0.4
	6.7	0.4	0.4	1.1					1.1	47.9				5.2	2.2	0.7		
	8.4	1.4		5.1	0.5					42.7	1.4			6.0	9.2	1.9		
	4.8	1.3	5.5	0.3				0.7	7.9	60.1		0.3			3.4	1.0		
	4.2		6.1	1.5	2.3				2.3	44.7				0.8	8.0			
	4.1	0.5	3.9	1.5					0.7	72.8		0.2						
	12.5		0.5	1.3						17.6					0.5			9.4
	19.8	2.4	5.1	1.6					2.8	49.1		1.6						
	12.4	1.8	3.2	0.9					2.3	56.6		2.3			1.4			
	5.2	1.1	4.4						0.8	73.0					4.5			
	2.9		1.4						1.8	46.1		2.1				0.5		
	8.2	1.5	2.5	1.0					0.5	80.8		1.5						
	7.8		2.2						2.2	26.7		1.1						
	8.4		0.5	1.4					1.9	38.3		2.8			0.9			0.5
	1.7	0.8	0.4	0.4				0.4	0.4	31.2		11.3	0.8		7.1			
	5.5	1.0	0.5	0.5					3.5	36.8		6.5	0.5		2.5			
	14.9		1.4	1.0					0.5	21.5		0.5						
	12.5	1.3	5.9	7.6				0.4	2.2	31.2		1.3	1.3					
	20.1	1.0	5.1	0.8					6.6	31.4		1.5	0.8		0.8		0.3	
	23.2	0.3	0.5	0.3					4.4	31.2		2.1						
	8.6		0.4						3.7	43.6		2.6						
	47.1		0.5	1.0					0.5	7.8		1.0						
	28.4		1.7	2.5						12.1		0.4						
	27.3			0.4					2.1	21.0		2.1	2.9					
	38.1	0.4	1.1	0.8					0.8	15.5		0.4	1.9		0.4		0.8	
	56.3		0.9						1.4	8.5		0.9	0.5					
	5.2	3.1	8.2	1.8					1.6	43.3		2.1						1.6
	10.3	2.8	5.4	0.3					3.8	45.0		1.8	2.4					
	9.5		1.0						1.0	13.5		0.5						
	4.9		0.4						1.6	34.4		2.4	8.9		2.9		1.2	
	3.5			0.3					1.1	23.6		1.6	5.5		0.8			0.3
	11.7		0.2						0.9	12.9		1.2	29.0		0.2	1.0		
	0.8	0.6	2.8	1.8					1.8	35.2		1.4	24.6					
	6.9		1.9						0.9	29.6		1.9	12.0		0.5			
1.6	12.2		2.6	3.7					1.5	51.6		1.5						0.4
	2.3								6.6	23.0		0.8	0.4					
	0.4		0.2						1.8	23.9								
	1.9		0.8	0.8					1.9	74.6		0.4						
1	45	22	41	33	8	1	3	40	45	6	37	15	8	24	10	5	6	
1.6	11.0	1.1	2.1	1.4	0.8	0.1	0.5	2.0	41.2	1.2	1.7	6.1	3.5	2.8	0.9	0.6	2.1	

Table 5 shows the relationship between the number of species in each lake and the various parameters of the water and sediment. There is no relationship between number of species and latitude. The correlation coefficient is not significant, and its positive value shows, if anything, that there tend to be more species in northern lakes than southern. There is also no significant difference between the mean number of species in each lake type, as shown by the *t* test between the extreme means in Table 5.

TABLE 4. Chydorid species found in each lake, and percentage composition of local faunas. Unknowns are included in the total fauna, unrecognizables are not—Continued.

No. lake, state	<i>Alonella hamulata</i>	<i>Alonella globulosa</i>	<i>Alonella dadayi</i>	<i>Alonella</i> sp.	<i>Leydigia leydigi</i>	<i>Leydigia acanthocerooides</i>	<i>Anchistropus minor</i>	<i>Monospilus dispar</i>	<i>Dunhevedia crassa</i>	<i>Dunhevedia serrata</i>	<i>Euryalona occidentalis</i>	Unknown	Unrecognizable	Total chydorids
1. Itasca, Minn.	--	---	---	---	1.3	---	---	---	---	---	---	0.3	10.6	309
2. Big Pelican, Minn.	--	---	---	---	1.2	---	0.3	---	---	---	---	---	10.7	327
3. Ruth, Minn.	--	---	---	---	1.3	---	---	0.1	---	---	---	1.9	5.8	677
4. Little Rock, Minn.	--	---	---	---	1.9	0.3	---	---	0.1	---	---	0.5	2.5	731
5. Brigg's, Minn.	--	---	---	---	2.0	---	---	---	---	---	---	---	3.9	440
6. Big, Minn.	--	---	---	---	1.3	---	---	---	---	---	---	---	4.5	398
7. White Clay, Wis.	--	---	---	---	0.6	0.3	---	0.6	---	---	---	0.3	5.6	338
8. James, Ind.	--	---	---	---	4.3	---	0.4	---	---	---	---	---	7.8	231
9. Crooked, Ind.	--	---	---	---	6.3	---	---	---	0.4	---	---	0.4	4.9	269
10. Pleasant, Ind.	--	---	---	---	---	---	---	---	---	---	---	---	11.2	215
11. Hamilton, Ind.	--	---	---	---	---	---	---	---	---	---	---	---	7.5	293
12. Chapman, Ind.	--	---	---	1.1	1.1	0.4	---	---	1.5	---	---	1.1	7.3	262
13. Storey, Ill.	2.4	---	---	---	8.2	---	---	---	---	---	---	---	6.1	409
14. Springfield, Ill.	0.5	---	---	0.5	39.5	5.8	---	---	---	---	---	0.5	7.6	223
15. Lenape, Ind.	--	---	---	---	40.1	---	---	---	---	---	0.4	---	4.4	252
16. Shakamak, Ind.	--	---	---	---	4.7	0.5	---	---	---	---	---	---	5.9	219
17. Starve Hollow, Ind.	0.4	---	---	---	1.9	---	---	---	---	---	0.4	---	1.5	265
18. Horseshoe, Mad., Ill.	--	---	---	---	27.4	6.8	---	---	---	0.4	---	0.7	3.2	281
19. Geneva, Ind.	--	---	---	---	---	---	---	---	---	---	---	---	0.5	264
20. Carbon, Ill.	2.2	---	---	---	43.3	5.4	---	---	---	---	---	3.3	1.1	90
21. Little Grassy, Ill.	0.5	---	---	---	22.3	7.5	---	---	---	---	---	0.9	3.7	214
22. Otter Pond, Ill.	--	2.5	---	---	0.8	---	---	---	---	0.4	---	---	1.7	240
23. Horseshoe, Ill.	1.5	0.5	---	---	14.9	10.8	---	---	---	---	---	---	5.5	201
24. Reelfoot, Tenn.	--	---	---	---	30.8	7.2	---	---	---	---	0.5	---	5.8	208
25. Stave, Ark.	--	---	---	---	13.9	8.9	---	---	---	3.1	---	---	11.2	224
26. Horseshoe, Ark.	0.5	---	---	---	6.5	5.4	---	---	---	---	---	0.5	8.9	392
27. Annette, Miss.	1.5	---	---	---	21.4	9.0	---	---	---	---	---	---	2.1	389
28. Alligator, Miss.	21.6	---	---	---	3.0	6.0	---	---	---	---	0.4	---	9.3	268
29. Washington, Miss.	2.4	---	---	---	13.6	10.6	---	---	---	---	---	---	13.5	287
30. Providence, La.	5.0	---	---	---	23.0	7.1	---	---	---	---	---	---	9.2	239
31. St. Joseph, La.	1.2	---	---	---	2.9	10.3	---	---	7.0	5.8	2.1	---	12.4	242
32. Bruin, La.	1.1	---	---	0.4	15.9	1.9	---	---	---	---	---	0.8	17.4	264
33. St. John, La.	5.6	---	---	---	6.6	1.9	---	---	---	---	1.4	---	11.4	210
34. Cane River, La.	17.5	---	---	---	3.1	2.1	---	---	---	---	2.7	0.8	7.7	376
35. Concordia, La.	5.2	0.3	---	---	5.4	1.5	0.3	---	1.5	---	2.1	1.2	8.9	326
36. Horseshoe, La.	19.2	---	---	---	22.5	23.6	---	---	---	---	1.0	0.5	24.6	208
37. Bennet's, La.	12.3	---	13.1	---	1.2	3.3	---	---	0.8	---	---	4.9	15.5	245
38. Miller's, La.	2.4	---	---	---	3.7	7.1	---	---	---	---	3.2	0.5	8.7	380
39. Chicot, La.	4.6	0.1	6.9	---	---	0.1	0.1	---	4.6	0.7	---	2.7	8.4	922
40. Cannon's, La.	1.0	---	---	---	0.8	0.2	---	---	2.0	1.0	3.2	0.6	6.5	506
41. Cazan's, La.	0.5	---	0.9	---	2.8	---	---	---	---	---	3.2	0.9	11.1	217
42. False River, La.	1.1	---	---	---	3.7	1.1	---	---	0.7	---	1.1	1.5	17.0	271
43. Dun-Roamin, La.	20.6	---	---	---	1.9	1.9	---	---	---	---	25.3	4.3	14.0	257
44. Lake Vue, La.	62.1	---	---	---	2.8	1.3	---	---	---	---	4.7	0.9	6.6	443
45. Audubon, La.	2.7	---	---	---	2.3	8.7	---	---	---	---	1.9	1.5	7.6	262
No. of occurrences	26	4	3	3	41	30	4	2	9	6	16	24	45	----
Mean abundance where found	7.5	0.9	7	.6	10.0	5.2	0.3	0.4	2.6	1.9	3.4	1.3	8.2	----

Although more species can be expected in natural waters than in either artificial or oxbow lakes, the latter two have about the same mean number of species.

Significant correlations were found between numbers of species and relative amounts of organic matter both in the sediments and in the water. Since it has already been shown (see Description of Lakes) that both these parameters are correlated with latitude but in opposite directions, the

TABLE 5. Number of species *vs* various parameters.

Number of spp. <i>vs</i> :	d.f.	correlation coefficient <i>r</i>	regression coefficient <i>b</i>
Latitude	43	0.202	
Alkalinity (me)	42	0.265	
TDS (mg/L)	42	0.257	
% dissolved organic matter	42	0.537**	1.04**
% sedimentary organic matter	43	0.291**	0.83**
mg/L dissolved organic matter	42	-0.280	
mg/cc sedimentary organic matter	43	-0.023	
Lake types		mean, no. spp.	<i>t</i>
Natural	14	16.9	0.533
Artificial	17	13.9	
Oxbow	11	14.3	

** = significant at 1% level or less.

paradox involved here of number of species being positively correlated with both these parameters but not with latitude cannot be elucidated at this point. It is an area that suggests itself for future investigations and indeed may become critical in studies involving the chydorids as indicators of productivity. However, the correlations of number of species with alkalinity and TDS are not significant. Likewise there is no correlation between the number of species and productivity to the extent that the latter is indicated by alkalinity or TDS.

The percent composition of the species of the chydorids is the only logical basis for comparison in this study, since the populations of remains fluctuate so widely in absolute abundance. This method of presentation shows the relative importance of each species in relation to the total fauna. In this way a strict comparison between lakes is feasible.

Most species in the study occurred over the whole range of the transect, although some were obviously restricted in their distribution to either the north or south. Three distributional categories can be defined. 1) Eurytopic species are those that are distributed over the whole transect and whose relative abundance is not significantly correlated with latitude. 2) Northern species are those whose importance in the fauna decreases significantly southward. 3) Southern species are those whose importance in the fauna decreases significantly toward the north. Only 24 species of chydorids in this study occurred consistently enough to enable a statistical analysis to be made of their distribution patterns.

The most common and widely distributed chydorid in the Mississippi Valley is *Chydorus sphaericus*. It occurred in every lake studied, and its remains dominated the microfossil populations in nearly all the lakes. The correlation coefficient *r* of *sphaericus* with latitude is 0.599**, 43 d.f. The regression equation is $y = 2.42^{**}x - 47.9$, with a standard error of the slope *s_b* of 0.38. The mean abundance of the species in the sediments was 41.2%.

The great abundance of *C. sphaericus* and its significant decrease with latitude has an effect upon the relative abundance of the other species.

TABLE 6. Adjusted percentages of chydorids in each of the local faunas. Percentages are based on total chydorid remains minus those of *Chydorus sphaericus*.

No., lake, state	<i>Acroperus harpae</i>	<i>Alona quadrangularis</i>	<i>Alonella excisa</i>	<i>Graptoleberis testudinaria</i>	<i>Alona karua</i>	<i>Alonella hamulata</i>	<i>Camptocercus rectirostris</i>	<i>Leydigia acanthocercoides</i>	<i>Alona rectangulara</i>	<i>Chydorus globosus</i>	<i>Leydigia leydigii</i>
1. Itasca, Minn.	3.6	16.7	3.6	0.7	---	---	0.7	---	9.4	1.4	2.9
2. Big Pelican, Minn.	11.3	3.9	10.0	3.9	---	---	6.1	---	4.2	1.3	1.7
3. Ruth, Minn.	2.9	16.8	3.5	0.6	---	---	1.2	---	4.1	---	5.3
4. Little Rock, Minn.	13.7	7.5	4.1	6.9	---	---	14.4	1.4	11.6	1.4	9.6
5. Brigg's, Minn.	22.6	4.3	2.2	---	---	---	11.8	---	1.1	---	9.7
6. Big, Minn.	19.5	13.3	3.5	1.8	---	---	4.4	---	3.5	0.9	4.4
7. White Clay, Wis.	11.7	6.8	5.4	3.4	---	---	4.9	0.5	6.4	1.0	1.0
8. James, Ind.	18.5	12.8	6.7	4.1	---	---	2.6	---	2.1	2.1	5.1
9. Crooked, Ind.	14.5	2.3	3.5	5.2	---	---	---	---	3.5	---	10.0
10. Pleasant, Ind.	9.5	1.4	13.6	6.8	---	---	0.7	---	4.8	---	---
11. Hamilton, Ind.	3.6	3.6	7.2	6.4	---	---	2.1	---	5.0	0.7	---
12. Chapman, Ind.	8.5	4.9	12.8	10.4	---	---	3.7	---	4.9	---	1.8
13. Storey, Ill.	---	---	---	---	---	7.4	0.7	---	14.0	0.7	25.0
14. Springfield, Ill.	---	2.0	0.5	0.5	---	0.5	0.5	14.9	9.5	---	43.8
15. Lenape, Ind.	---	2.9	---	5.0	0.7	---	5.0	---	6.5	2.9	7.2
16. Shakamak, Ind.	---	---	2.8	1.8	2.8	---	3.7	0.9	16.5	4.6	9.2
17. Starve Hollow, Ind.	1.3	---	15.8	3.9	---	1.3	2.6	---	7.9	---	6.6
18. Horseshoe, Mad., Ill.	---	8.1	---	---	0.6	---	---	11.9	7.5	3.7	48.2
19. Geneva, Ind.	---	2.5	---	---	---	---	---	---	7.5	7.5	---
20. Carbon, Ill.	---	3.0	---	---	---	3.0	---	6.0	7.5	1.5	56.7
21. Little Grassy, Ill.	---	11.4	1.4	---	---	0.7	2.1	11.4	5.0	4.3	34.2
22. Otter Pond, Ill.	---	0.6	10.0	1.8	41.9	---	7.7	---	---	15.9	1.2
23. Horseshoe, Ill.	---	2.9	3.6	---	7.3	2.2	2.2	16.0	1.4	9.4	21.8
24. Reelfoot, Tenn.	---	6.9	---	---	1.1	---	1.7	8.6	13.1	0.6	36.6
25. Stave, Ark.	---	3.3	---	---	7.8	---	---	11.2	1.7	1.7	17.3
26. Horseshoe, Ark.	---	6.9	1.0	---	5.6	0.6	3.9	6.9	4.6	2.0	8.2
27. Annette, Miss.	---	4.0	---	---	---	2.2	---	12.7	2.5	2.9	30.1
28. Alligator, Miss.	---	0.6	---	---	4.5	33.0	2.3	9.1	6.3	4.0	4.6
29. Washington, Miss.	---	3.6	---	---	---	2.3	5.0	10.0	5.9	0.9	12.8
30. Providence, La.	---	3.4	---	---	---	5.2	2.2	7.3	5.6	0.4	23.7
31. St. Joseph, La.	---	1.4	---	---	2.7	1.4	8.6	11.3	3.6	2.3	3.2
32. Bruin, La.	---	4.5	0.4	---	2.2	1.1	6.0	1.9	4.8	0.4	15.6
33. St. John, La.	---	3.7	---	---	---	5.6	5.1	1.9	6.9	0.9	6.5
34. Cane River, La.	---	---	---	---	3.7	27.3	5.4	3.3	0.8	3.3	5.0
35. Concordia, La.	---	4.3	---	---	1.0	8.2	10.1	2.4	1.0	2.9	8.7
36. Horseshoe, La.	---	0.9	---	---	---	17.3	0.9	20.8	4.8	0.4	20.4
37. Bennet's, La.	0.5	0.5	3.5	---	3.5	15.0	0.5	4.0	1.5	3.0	1.5
38. Miller's, La.	---	4.0	0.9	---	13.7	2.8	13.0	8.4	1.2	1.9	4.3
39. Chicot, La.	---	0.3	0.2	---	17.7	4.8	3.6	0.1	---	1.3	---
40. Cannon's, La.	---	---	---	---	27.4	1.4	2.5	0.3	---	1.9	1.1
41. Cazan's, La.	---	---	0.6	---	22.5	0.6	2.2	---	2.2	2.2	3.4
42. False River, La.	---	0.6	---	---	4.5	1.7	19.8	1.7	1.1	2.3	5.7
43. Dun-Roamin, La.	---	3.0	---	---	0.4	22.4	2.6	2.2	3.0	0.9	2.2
44. Lake Vue, La.	---	0.3	---	---	0.3	81.6	0.6	1.8	0.3	---	3.9
45. Audubon, La.	---	3.0	---	---	1.5	10.8	4.6	35.4	1.5	1.5	9.2

The relative abundance of species in the South is magnified to the extent that the decrease in dominance of *sphaericus* allows this. Conversely, the relative abundance of species in the north is depressed by the overwhelming dominance of *sphaericus*. For this reason adjusted percentages were calculated for each of the 23 species treated statistically by eliminating *sphaericus* from the totals. These data are given in Table 6.

With these adjusted data it is possible to calculate more realistic correlation coefficients and regressions. These statistics and other pertinent data are listed in Table 7, in which the species are grouped alphabetically.

No regression equations were calculated for those species that did not have a significant correlation with latitude. Where a species occupied a restricted latitudinal range, only those values of abundance, including zero values, over that range were used in the calculations. The adjusted mean abundance was calculated on this same basis.

Several species that were restricted to either the north or south had an r value not significant at the 5 percentile level. Despite this they are not eurytopic according to the definition previously given. The range of species such *Alonella nana*, *Chydorus faviformis*, and *Pleuroxus procurvus* show this very well. These are restricted to a region from the Indiana Lake District northward. The same is true of *Graptoleberis testudinaria*: it occurred 16 times down to 37.50°N , but 15 of these were north of 38.84°N . These last four named species even though they technically fall into the eurytopic group are really northern species and will be so considered. An opposite situation exists in the case of *Alonella hamulata*, which does not occur north of the Indiana Lake District. It is abundant and occurs consistently south of there; hence, it is classed here as a southern form.

Those species with significant negative r values are considered southern species and those with positive r values are northern at least along the present latitudinal transect. All regression coefficients were significant above the 1 percent level.

The grouping called small *Alona* in Table 4 comprises shells and/or head shields that are often difficult or impossible to identify at the species level. Included here are *A. rectangula*, *A. guttata*, *A. costata*, *A. intermedia*, *A. verrucosa*, and possibly *A. monocantha*. Since it is impossible to divide the small *Alona* category proportionately among the species known to occur in a lake it was decided to leave the group as it stands. A proportional division of the small *Alona* group would in all probability not influence the slope of the regressions involved, nor would it influence the correlation coefficient.

The grouping, *Chydorus* spp., is a unique case. This comprises a group of species that so far cannot be separated from one another on the basis of the morphology of the remains. It is suspected that at least 3 species are involved in this group—*barroisi*, *hybridus*, and *poppei*—although there may be another species involved hitherto unreported from North America or possibly even undescribed. Still the distribution is uniform in that lumping the species into a complex results in a significant correlation and regression. All but one of the occurrences are south of 38°N . The southern affinity of this group and its importance in Cazan's, Cannon's, and Chicot Lakes, Louisiana, made it an important indicator group.

TABLE 7. Regression equations, correlation coefficients and other statistical analyses of chydorid species. The species are grouped according to decisions made concerning their latitudinal affinities.

Species	Latitudinal range	No. of occurrences	Adjusted mean abundance \bar{y}	Correlation coeff. (r)	Regression equation $y =$	Std. error of slope (S_b)	Mean square deviation from regression ($S_y \cdot x^2$)
Eurytopic species							
1. <i>Alona rectangula</i>	47.08	42	5.1	0.251			
2. <i>Camptocercus rectirostris</i>	47.08	39	4.0	-0.058			
3. <i>Chydorus globosus</i>	47.08	37	2.2	-0.087			
4. <i>Leydigia leydigi</i>	47.08	41	11.7	-0.036			
5. <i>Pleuroxus denticulatus</i>	47.08	41	3.9	0.181			
Northern species							
6. <i>Acropervus harpae</i>	47.08	14	3.2	0.682**	$0.78^{**}x - 25.6$	0.1169	4.22
7. <i>Alona quadrangularis</i>	47.08	37	4.1	0.567**	$0.45^{**}x - 12.5$	0.0680	2.46
8. <i>Alonella excisa</i>	47.08	24	2.6	0.518**	$0.39^{**}x - 11.6$	0.0591	2.13
9. <i>Eurycercus lamellatus</i>	47.08	24	2.7	0.427**	$0.30^{**}x - 8.4$	0.0542	1.63
10. <i>Graptoleberis testudinaria</i>	47.08	16	2.9	0.123			
Southern species							
11. <i>Alona karua</i>	39.17	22	3.9	-0.306*	$-0.47^{**}x + 21.2$	0.0716	2.58
12. <i>Alonella hamulata</i>	41.00	26	7.9	-0.335			
13. <i>Chydorus</i> spp.	46.58	15	2.6	-0.380*	$-0.50^{**}x + 21.0$	0.0762	2.75
14. <i>Euryalona occidentalis</i>	39.17	16	2.4	-0.410*	$-0.65^{**}x + 24.5$	0.1196	2.13
15. <i>Leydigia acanthocercoides</i>	45.75	30	5.0	-0.382*	$-0.50^{**}x + 23.4$	0.0763	2.76
Other species							
<i>Alona affinis</i>	47.08	34	2.5	0.527**	$0.32^{**}x - 9.3$	0.0481	1.74
<i>Alona guttata</i>	47.08	12	0.4	0.418**	$0.06^{**}x - 1.9$	0.0098	0.35
<i>Alonella exigua</i>	47.08	10	0.3	0.419**	$0.06^{**}x - 1.9$	0.0270	0.97
<i>Alonella nana</i>	47.08	8	4.4	0.051			
<i>Chydorus faviformis</i>	47.08	6	1.0	0.095			
<i>Kurzia latissima</i>	47.08	40	3.0	-0.138			
<i>Pleuroxus procurvus</i>	46.58	8	0.9	-0.204			
<i>Pleuroxus trigonellus</i>	47.08	22	1.1	0.140			

* = 5% level of significance or less.

** = 1% level of significance or less.

While it might seem desirable to use all species in determining whether the chydorid fauna of a given lake is dominated by northern or southern forms, this approach is not practical. First, some species are too rare to treat statistically and arrive at a decision concerning their affinity. Second, the resulting system would be too cumbersome. Third, since *Chydorus sphaericus* is overwhelmingly dominant in most lakes, its inclusion would de-emphasize fluctuations in relative abundance of the other species. For this reason *sphaericus* is not included in the ensuing discussion, which attempts to set up criteria for selecting species to serve as indicators of latitudinal assemblages.

The 23 species presented in Table 6 form a good nucleus for deciding the affinities of the chydorid fauna of any particular lake. In order to make a list comprising equal numbers of species from each of the three groups—eurytopic, northern, and southern—the group with the fewest number of species limits the size of the list. Since there are only 5 southern species in Table 6, it was decided to choose 5 eurytopic and 5 northern species. The list of indicator species thus contain 15 species of the 24 analyzed statistically. An attempt was made to diversify the groups as much as possible.

Thus the only species of eurytopic *Pleuroxus* chosen was *denticulatus*, since it was more abundant and occurred more often than *trigonellus*. *Alona affinis* and *A. quadrangularis* are closely related species, of which *A. quadrangularis* was chosen for the same reason. *Kurzia latissima* was omitted from the eurytopic indicator group on a purely arbitrary basis. The only species it could logically replace in the indicator group is *C. globosus*, since it occurs more often and is more abundant than *globosus*. But the exceedingly low correlation coefficient of *C. globosus* made it a better choice than *Kurzia* as an indicator of eurytopic species.

Based only on the remains of the indicator species recovered, the relative abundance (percentage) of each of the 15 species for each lake was calculated. From these percentages bar graphs were constructed for each lake which show the changing composition of the chydorid fauna from north to south as demonstrated by these 15 indicator species.

Figure 2 shows two "typical" northern patterns. The first, White Clay Lake, Wisconsin shows:

Eurytopic	32%
Northern	67%
Southern	1%

All five northern species are present and dominate the fauna. One southern species is present (*L. acanthocercoides*), which occurs sporadically in the north. The eurytopic species are as abundant as would be expected from the strictly random distribution of all species (33 $\frac{1}{3}$ %). Lake Chapman, Indiana shows essentially the same pattern:

Eurytopic	33%
Northern	66%
Southern	1%

These two lakes show a clear dominance of northern species. This was

KEY TO HISTOGRAMS

% = PERCENT OF INDICATOR GROUP

E = EURYTOPIC SPECIES



- 1 ALONA RECTANGULA
- 2 CAMPTOCERCUS RECTIROSTRIS
- 3 CHYDORUS GLOBOSUS
- 4 LEYDIGIA LEYDIGI
- 5 PLEUROXUS DENTICULATUS

N = NORTHERN SPECIES



- 6 ACROPERUS HARPAE
- 7 ALONA QUADRANGULARIS
- 8 ALONELLA EXCISA
- 9 EURYCERCUS LAMELLATUS
- 10 GRAPTOLEBERIS TESTUDINARIA

S = SOUTHERN SPECIES



- 11 ALONA KARUA
- 12 ALONELLA HAMULATA
- 13 CHYDORUS SPP.
- 14 EURYALONA OCCIDENTALIS
- 15 LEYDIGIA ACANTHOCERCOIDES

the case in all lakes studied in the Indiana Lake District, the one lake in Wisconsin, and 5 of 6 lakes studied in Minnesota.

The inverse condition prevailed in lakes with a dominant southern fauna. Alligator Lake, Mississippi, shown in Figure 2, is a "typical" southern lake. Not all 5 southern indicator species are present, however, in that the *Chydorus* spp. complex is absent, as it also is in Audubon Lake, Louisiana. The latter lake shows another "typical" pattern of southern dominance.

The faunas of the lakes at the extremes of the transect were easily classified on the basis of the indicator species. However, it is difficult to define quantitatively the zone of overlap where the northern and southern faunas interdigitate. It was apparent that no line of faunal balance could conveniently be drawn, and even a zone of overlap could not be described on the basis of the bar graphs such as those that have been presented.

A more quantitative method was clearly needed, and for this purpose regressions were again utilized. The regression of the percentage of each group *vs* latitude was calculated (Fig. 3), for which the pertinent statistics are presented in Table 8. The resulting regressions crossed at 37.50°N, and this nearly coincides with the median latitude of the transect (38.50°N). While these regressions give an indication of the crucial area

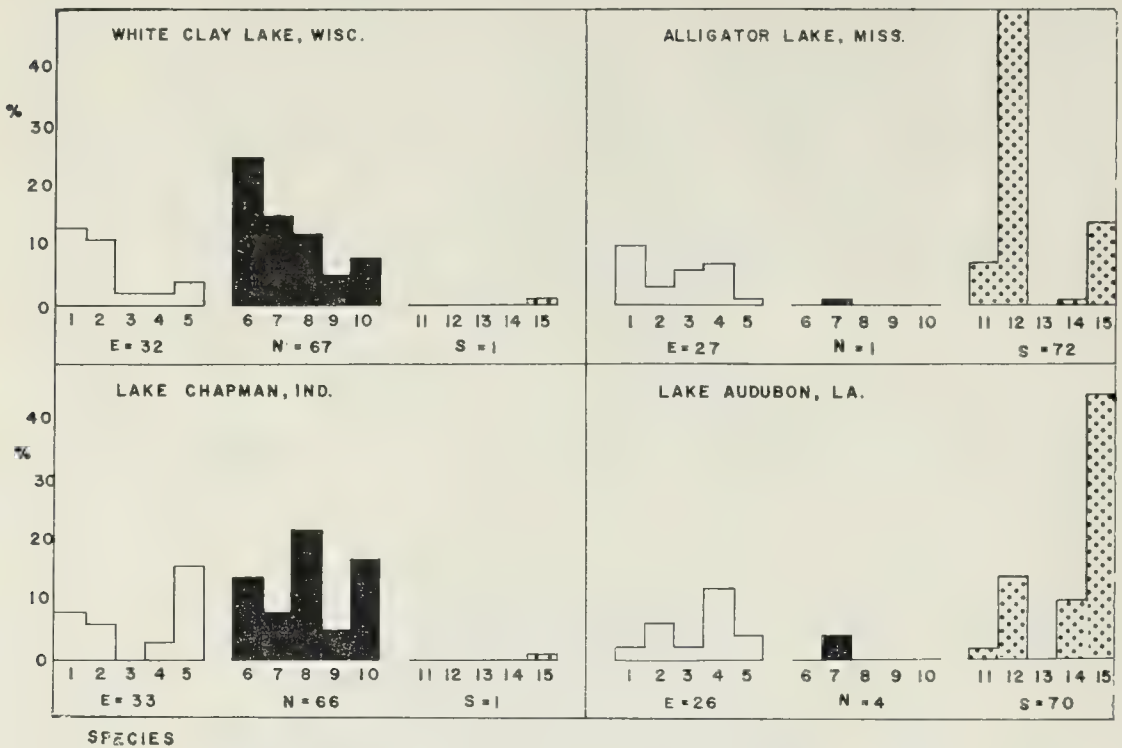


FIG. 2. Histograms showing percentage of each indicator species for two lakes with dominance of northern species and two with dominance of southern species.

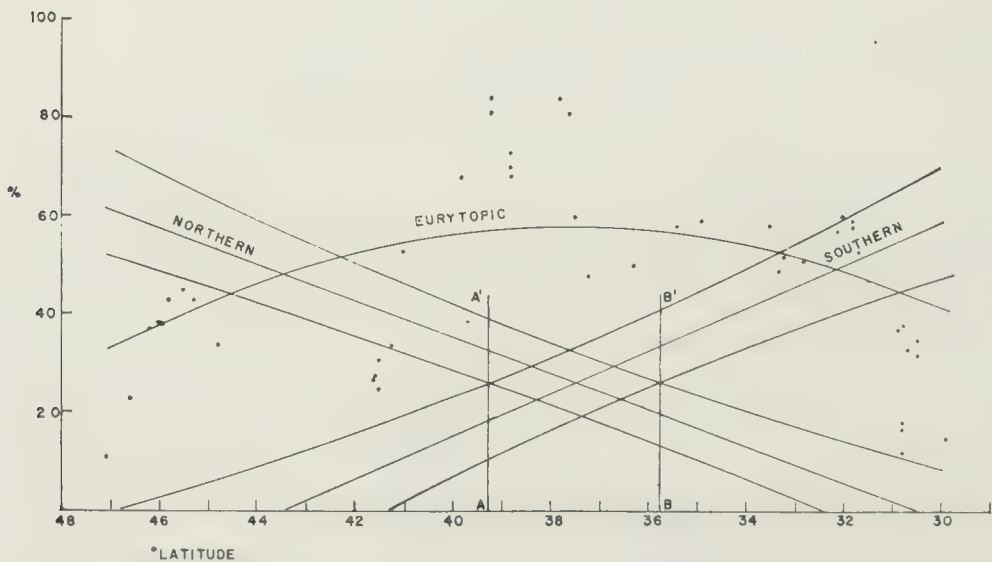


FIG. 3. Regressions of northern and southern indicator groups vs latitude with their 95% confidence limits. Isolated points represent running means of eurytopic group. Curve of eurytopic species was fitted to these points by inspection.

of overlap of the faunas, they do not define its extent. When the 95% confidence limits are calculated and plotted, the resulting intercepts cover an area over the median portion of the latitudinal abscissa. The region of overlap, indicated by the vertical lines AA' and BB' in Figure 3, extends from 35.80°N to 39.25°N, a distance of 3.45° of latitude. Geo-

TABLE 8. Three groups of chydorid indicator species and the statistics of their regressions *vs* latitude.

Group	Mean % abundance	Correlation coefficient (<i>r</i>)	Regression equation <i>y</i> =	Std. error of slope (<i>S_b</i>)
Eurytopic	46.7	0.098		
Northern	24.1	0.764**	3.68** <i>x</i> —111.7	0.560
Southern	28.8	—0.804**	—4.36** <i>x</i> +189.6	0.665

** = significant at 1% level or less.

graphically this extends from the region of northeast Arkansas to a line just south of Terre Haute, Indiana.

The eurytopic group of indicator species showed no significant correlation with latitude, as expected by definition. Moving averages of 3 were computed for this group of species and are plotted in Figure 3. A curve fitted by inspection to these points has its peak over the median portion of the transect. Hence, the eurytopic species are numerically dominant in the zone of overlap.

It is now necessary to ascertain whether individual lakes in the overlap region as defined on a statistical basis actually do have a eurytopic fauna dominant over either a northern or southern one. The lake closest to the southern boundary of the zone of overlap is Stave Lake, Arkansas, at 35.42°N, and the lake closest to the northern boundary is Lake Lenape, Indiana, at 39.17°N. This zone contains 11 lakes in this study, the graphs for which are presented in Figures 4-6.

In Stave Lake, Arkansas, the southern species are nearly as abundant as the eurytopic ones, and the northern forms are at a very low level (Fig. 4). Comparison with the other faunas graphed in Figure 4 shows essentially the same situation except for Otter Pond, Illinois, in which the southern species predominate. Still the situation is one of dominance by eurytopic forms, with southern species being more abundant than northern. Figure 5 for lakes somewhat further north shows a continuation of the eurytopic dominance. The relative abundance of southern and northern species is about equal in Little Grassy, Carbon Lake, and Horseshoe Lake at Madison, Ill., but in Starve Hollow Lake, Indiana, the northern forms are much more abundant than the southern species.

Lakes Shakamak and Lenape, Indiana, in Figure 6 show eurytopic dominance, with a slight preponderance of northern species over southern. These two lakes are very near the northern boundary of the statistically defined zone of overlap. Lake Geneva, Indiana, was not shown because of the extreme dominance of eurytopic species, a low number of species, and an imbalance of the chydorid fauna evident in the lake.

However, the trend established through the Zone of Statistical Overlap of dominance by eurytopic forms with decreasing importance of southern species from south to north is reversed in the two lakes immediately north of the Zone of Statistical Overlap (Fig. 6). Lakes Springfield and Storey, Illinois, show essentially the same pattern—

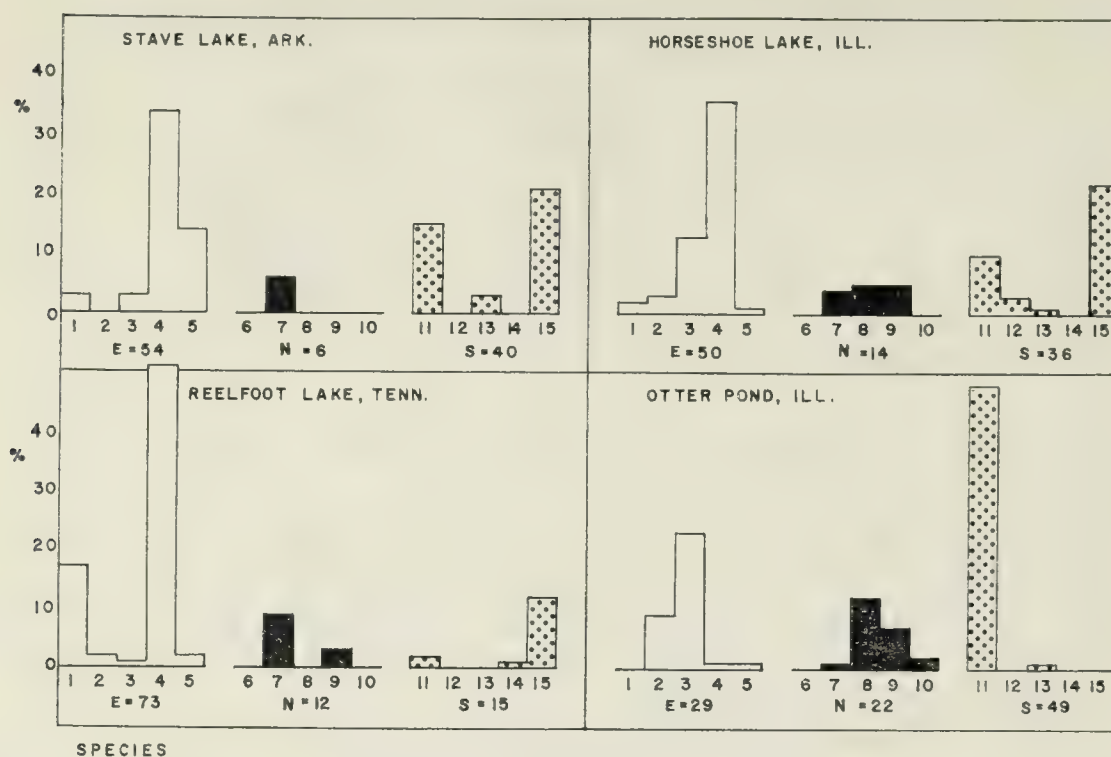


FIG. 4. Histograms showing percentage of each indicator species in various lakes in the Zone of Statistical Overlap.

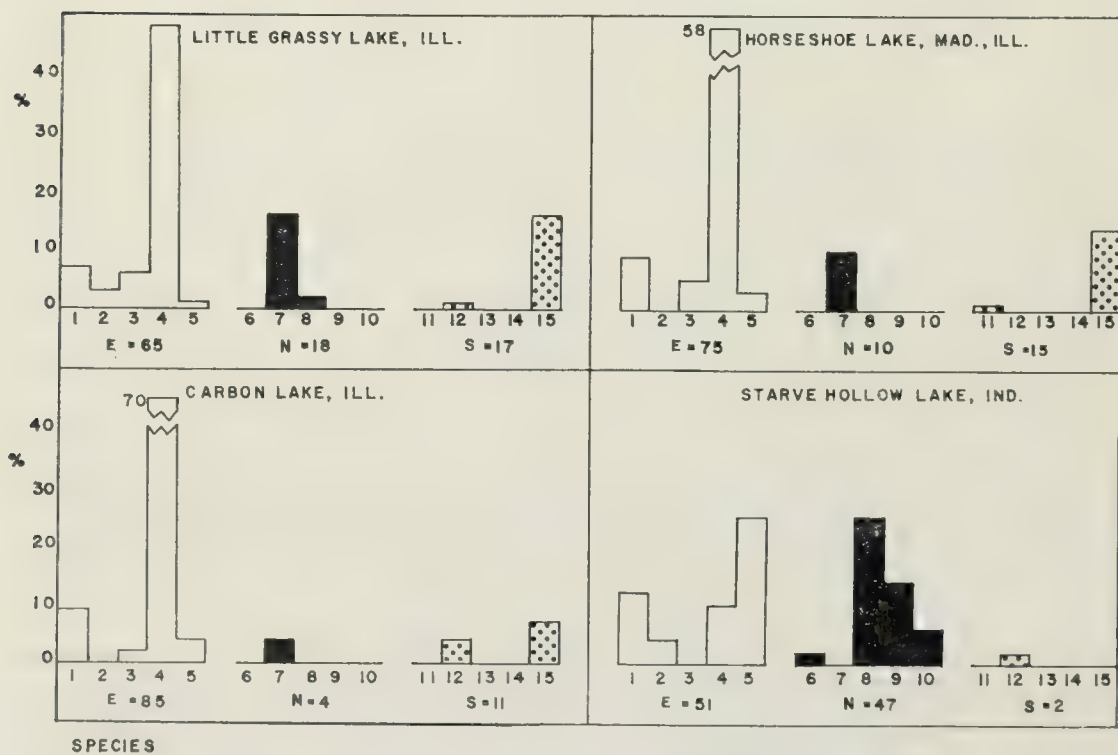


FIG. 5. Histograms showing percentage of each indicator species in various lakes in the Zone of Statistical Overlap.

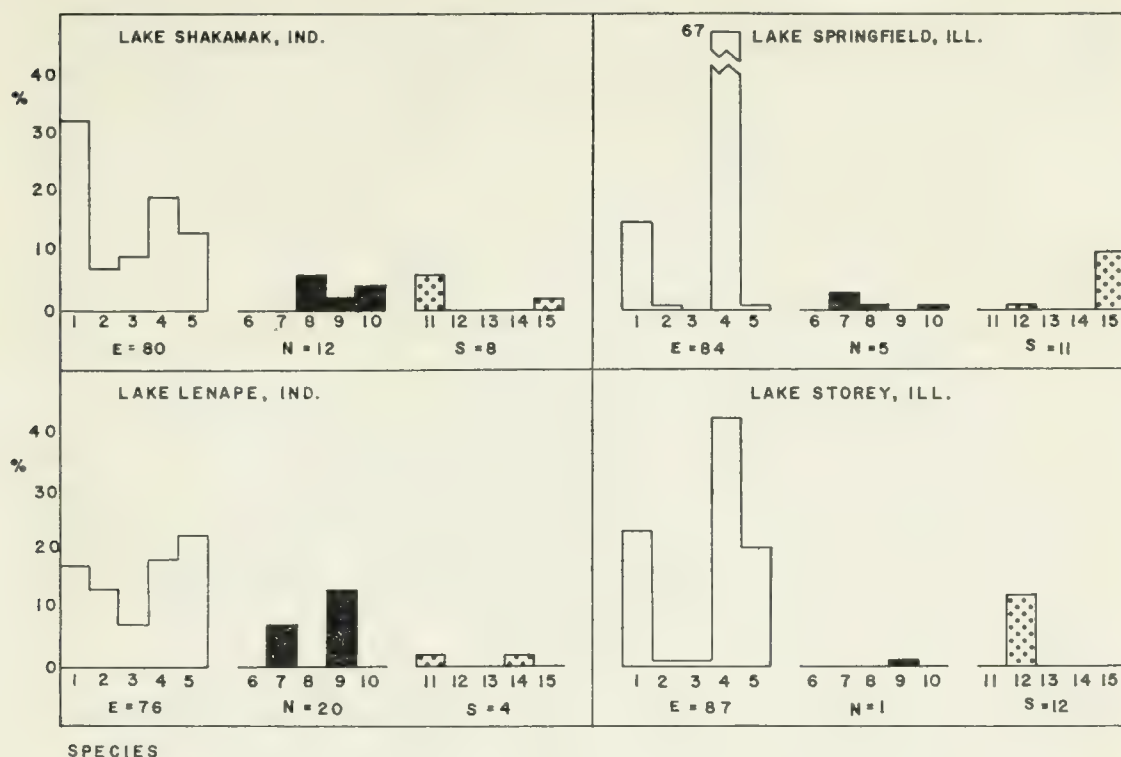


FIG. 6. Histograms showing percentage of each indicator species. Lakes Shakamak and Lenape in Indiana are in the Zone of Statistical Overlap. Lakes Springfield and Storey in Illinois are just north of this zone.

extreme dominance by eurytopic species—but the southern species again are more abundant than the northern ones.

The graph for Lake Chapman, Indiana, has already been presented as a “typical” northern fauna. The transition from the Zone of Statistical Overlap to the Northern Zone is abrupt. The eurytopic species dominate in the Zone of Statistical Overlap, and with the exception of lakes Spring-

TABLE 9. Percentage composition of groups of indicator species in lakes of the Northern Zone, arranged in order of decreasing latitude.

No., lake, state	Percent		
	Eurytopic	Northern	Southern
1. Itasca, Minn.	34	66	0
2. Big Pelican, Minn.	34	65	1
3. Ruth, Minn.	36	64	0
4. Little Rock, Minn.	60	38	2
5. Brigg's, Minn.	40	60	0
6. Big, Minn.	28	72	0
7. White Clay, Wisc.	32	67	1
8. James, Ind.	19	81	0
9. Crooked, Ind.	29	71	0
10. Pleasant, Ind.	26	74	0
11. Hamilton, Ind.	39	61	0
12. Chapman, Ind.	33	66	1
Mean	34.2	65.4	0.4

field and Storey there appears to be a gradual decrease in the southern fauna from south to north, which is accompanied by an increase in the eurytopic species rather than the northern forms.

Table 9 presents the percentage composition of each group of indicator species for the lakes of the Northern Zone. These data show a pronounced dominance by northern species, with southern forms either completely absent or present in extremely low abundance. The only exception to the established pattern is Little Rock Lake, Minnesota, which shows a pattern typical of lakes in the Zone of Statistical Overlap. There is no apparent reason for this exception.

The percentage compositions of the faunas in lakes south of the Zone of Statistical Overlap evince no corresponding abrupt change in dominance. Instead there is a Transition Zone in which the eurytopic species continue to be dominant, but in which there are two lakes in which southern species are dominant (Table 10). Further south there is a zone where southern species are consistently dominant, with the exception of two lakes (Table 12).

TABLE 10. Percentage composition of groups of indicator species in lakes of the Transition Zone, arranged in order of decreasing latitude.

No., lake, state	Percent		
	Eurytopic	Northern	Southern
26. Horseshoe, Ark.	52	19	29
27. Annette, Miss.	68	4	28
28. Alligator, Miss. ¹	27	1	72
29. Washington, Miss.	61	9	30
30. Providence, La.	65	7	28
31. St. Joseph, La. ¹	45	3	52
32. Bruin, La.	69	12	19
33. St. John, La.	61	11	28
Mean	56.0	8.3	35.8
Mean minus lakes with southern species dominance	62.7	10.3	27.0

¹ Fauna dominated by southern forms.

Table 11 compares the groups of indicator species in lakes in the Transition Zone and the Zone of Statistical Overlap. The differences between the faunas of the two zones are not great, but they are consistent with general trends. The eurytopic species are seen to decrease in abundance southward, although they are still dominant. The northern species decrease also, and there is a marked increase in the abundance of the southern species.

It does not appear that the zones should be combined. The differences seem to warrant keeping them apart. In the Transition Zone the southern species reach a real dominance over the northern species, and there is a progressive decrease in the dominance of the eurytopic forms toward

TABLE 11. Comparison of means of groups of indicator species of Statistically Defined Zone of Overlap and of Transition Zone. The figures in parentheses exclude those lakes with southern dominance, which are Otter Pond (22) in the Zone of Overlap, and Alligator (28) and St. Joseph (31) in the Transition Zone.

Zone	Percent		
	Eurytopic	Northern	Southern
Overlap ¹	69.3 (72.7)	13.8 (13.1)	16.9 (14.3)
Transition	56.0 (62.7)	8.3 (10.3)	35.8 (27.0)

¹ Includes lakes Springfield and Storey, Ill.

the south. Most of the increase in abundance of the southern species in the Transition Zone is at the expense of the eurytopic ones. Conversely, the increase in abundance of the eurytopic forms in the Zone of Statistical Overlap is at the expense of the northern forms.

At the extreme south is another region, analogous to the Northern Zone, in which the fauna is dominated by southern forms. Table 12 summarizes the data for this Southern Zone. Lakes Concordia and False River do not conform to the pattern set by other lakes in this zone in that the eurytopic species are dominant. Lake Concordia might logically belong in the Transition Zone, since it is quite close to Lake St. John, Louisiana. Both Lake St. John and Cane River Lake lie at the same latitude but they are quite far apart (See Table 1).

The four faunal zones established by this study are: The Northern Zone which includes lakes in the Indiana Lake District, Wisconsin, and

TABLE 12. Percentage composition of the groups of indicator species in lakes of the Southern Zone, arranged in order of decreasing latitude.

No., lake, state	Percent		
	Eurytopic	Northern	Southern
34. Cane River, La.	42	0	58
35. Concordia, La. ¹	58	8	34
36. Horseshoe, La.	40	2	58
37. Bennet's, La.	15	13	72
38. Miller's, La.	30	18	52
39. Chicot, La.	9	5	86
40. Cannon's, La.	11	0	89
41. Cazan's, La.	17	19	64
42. False River, La. ¹	77	1	22
43. Dun-Roamin, La.	13	5	82
44. Lake Vue, La.	6	1	93
45. Audubon, La.	26	4	70
Mean	28.7	6.3	65.0
Mean minus lakes with eurytopic species domi- nance	20.9	6.7	72.4

¹ Show dominance by eurytopic fauna.

TABLE 13. Mean abundance of groups of indicator chydorids in the four zones found in the Mississippi Valley.

Zones	Southern limit °N	Percent		
		Eurytopic	Northern	Southern
Northern	41.25	34.2	65.4	0.4
Statistical Overlap	35.42	69.3	13.8	16.9
Transition	31.75	56.0	8.3	35.8
Southern	29.92 ¹	28.7	6.3	65.0

¹ Southern limit of this study.

Minnesota; the Zone of Statistical Overlap, which includes the lakes shown in Figures 4-6; the Transition Zone, where eurytopic forms still dominate but southern species are gaining in abundance; and finally the Southern Zone last described. Table 13 summarizes the relative abundance of the groups of indicator chydorids in the various zones and indicates the southern limits of the zones.

DISCUSSION OF THE ZONATION

The indicator groups of species have shown that four zones along the transect of the Mississippi Valley can be recognized, each characterized by differences in the fauna. The method of statistical prediction based on regressions and their confidence limits of the groups proved to hold quite well for regions at the extremes of the transect. Statistical prediction, however, was not completely accurate for the middle section. The Zone of Statistical Overlap showed as predicted a dominance of eurytopic forms, with a sharp boundary between this and the Northern Zone. To the south the statistical prediction proved inadequate, and a further Zone of Transition became apparent, characterized by a gradual ascendancy of southern species to complete dominance in the Southern Zone.

It might be suggested that the sharp boundary at the southern limit of the Northern Zone is due to a difference in lake type. All lakes in this study north of 41.00°N are glacial in origin, whereas most of the lakes in the Zone of Statistical Overlap are artificial. Still the lakes in the latter zone that are of natural origin, whether or not oxbows, show a better balanced fauna. At the same time, of the five that fall into the natural category (also oxbows) only one, Otter Pond, Illinois, deviates from the predicted eurytopic dominance.

The lakes in the Zone of Transition do indeed show a gradual transition to dominance by southern forms as opposed to the sharp boundary where the Northern Zone begins. Table 1 shows that of the lakes in the Zone of Transition only Lake Annette, Mississippi, is artificial in origin. It shows a high abundance of eurytopic species. Also the abundance of northern species in this lake is lower than the mean for the zone, and hence the dominance of eurytopic forms in Lake Annette is at the expense of the northern species. This situation is similar to that of the lakes in the Zone of Statistical Overlap that also are artificial in origin.

It can be concluded that the sharp boundary existing between the Zone of Statistical Overlap and the Northern Zone is in part associated with the difference in the origin of the lakes. The glacial lakes of the north are naturally much older than any artificial lakes, and ecological conditions undoubtedly are in better balance. Therefore the chydorid fauna has had a longer period in which to become balanced and better established. This is not to say that all artificial lakes show an imbalance in the chydorid fauna, but many of those in question do, *e.g.* Lake Storey, Illinois, Lake Geneva, Indiana, and possibly Lake Springfield, Illinois. The other lakes of this zone, were they not artificial, would perhaps show a zone of transition similar to the one demonstrated in the south. Most assuredly this zone would not be as large as the southern zone, since there appears a bias for southern species to occur further north and in greater abundance than the inverse.

The time necessary for a chydorid fauna to become established in a new lake and then to become stabilized has not yet been investigated. However, a few guesses can be hazarded on the basis of the data presented here.

It is doubtful if any of the oxbow lakes studied are more than a few hundred years old (Fisk, 1944). Of the artificial lakes in the study, the ages of some of them are known. The data are summarized in Table 14, along with an estimate of the balance of the indicator fauna obtained by comparing the indicator fauna of the lake with the mean for lakes in its zone. If the indicator fauna deviated a good deal from the mean of the natural lakes around it, the fauna was considered unbalanced. This was especially true where a single indicator species dominated the fauna.

The first and obvious conclusion is that the older a lake is, the better balanced and more diverse is its chydorid fauna. A second striking conclusion is that a remarkably diverse fauna can develop quickly. For example, Lake Annette, Mississippi, although only 4 years old harbors 11 species, and the fauna although out of balance is not so badly so as might be expected. Also Lake Vue, Louisiana, was only 5 years old and contained 12 species; its indicator fauna was overbalanced in favor of

TABLE 14. Approximate ages and faunal balance of artificial lakes.

No., lake, state	Age	Total no. chydrorid spp.	Balance of indicator spp.
14. Springfield, Ill.	20	12	—
15. Lenape, Ind.	25	12	+
16. Shakamak, Ind.	31	15	+
18. Starve Hollow, Ind.	24	14	+
19. Geneva, Ind.	15	8	—
27. Annette, Miss.	4	11	—
40. Cannon's, La.	20	15	—
44. Lake Vue, La.	5	12	—
Mean —	13	12	
Mean +	28	14	

— = fauna approximately unbalanced
 + = fauna approximately balanced

southern species. A guess might be made therefore, based on these meagre data, that a lake does not have to be hundreds of years old to have a well established and diverse chydorid fauna. A conservative estimate would be 25 years, depending upon the proximity of the lake to other lakes and waterways.

The factors that influence this zonation can only be guessed at present. Non-conservative ecological influences could for the most part be ruled out, since the species comprising the indicator groups are found over wide ranges and are abundant. This would indicate wide ecological tolerances, and hence a really conservative influence must be sought. Climate seems to fit this requirement. Macro-climatic differences between adjacent areas are slight, and large areas share essentially the same climate.

The two most important components of climate are rainfall and temperature. Rainfall is abundant to heavy throughout the Mississippi Valley. It is not restricted seasonally, so that severe annual drought is not the rule. Moreover, all the lakes in this study are permanent. As has already been pointed out a great deal of clastic material is washed into oxbow and artificial lakes. This factor might cause an appreciable problem in turbidity, which might affect chydorid distribution. The single most striking climatic feature in the Mississippi Valley is the temperature gradient from north to south. In the extreme northern reaches of the Valley cool summers and severe winters prevail, whereas in the deep South mild winters and very hot summers are the rule.

The Hutchinson-Loeffler (1956) system of classification of lakes according to their turnover regimes suggests a possible avenue of approach. In their paper a thermal classification of lakes was proposed that considered latitude and altitude as the greatest influences upon this classification. A diagram is presented which shows an indistinct boundary at 40° latitude between those lakes that freeze during the winter (dimictic) and those that circulate throughout the winter (warm monomictic). In the interior of North America there seems to be a wide belt where lakes can be either dimictic or warm monomictic depending on the severity of the winter. Krumholz and Cole (1959) found this to be the case with Tom Wallace Lake, Kentucky, at a latitude of 38.08°N. Reelfoot Lake, Tennessee, has been known to freeze for long periods during severe winters.

Several factors such as morphometry, altitude, and degree of protection of the lake basin in addition to climate determine the thermal regime of a given lake. However, climate is the single most dominating factor. Two facets of climatic temperature would appear to influence the type of thermal regime set up in a temperate zone lake—mean minimum and mean maximum winter temperatures. The former determines whether an ice cover could be present, and if so whether it is likely to be intermittent or permanent could be estimated from mean maximum winter temperatures. In summer the extent of warming especially of the littoral zone could be estimated from mean minimum and maximum summer temperatures.

The lakes of the Indiana Lake District are dimictic, and the inverse winter stratification once established is usually of winter long duration.

TABLE 15. Mean minimum and maximum July and January temperatures (°F) for the Mississippi Valley at latitudes 35-38°.¹

State & latitude	Min. Jan.	Max. Jan.	Min. July	Max. July
Ind.				
38°	26	44	66	90
Ill.				
38°	26	44	66	90
37°	28	46	68	90
Mo.				
37°	26	46	68	92
36°	30	48	70	92
Ky.				
37°	28	46	68	90
36°	30	48	68	92
Tenn.				
36°	30	50	70	92
35°	32	50	70	92
Ark.				
36°	30	50	70	92
35°	32	52	70	92

¹ After Anderson, 1959; Dickson, 1960; Hickman, 1959; Joos, 1959; McQuigg, 1959; Schaal, 1959.

Further south the lakes in the region of 38°N fall into the category of irregular dimixis, which includes the lake studied by Krumholz and Cole.

The critical region from 38°N to somewhere south of Reelfoot Lake, Tennessee appears to be the belt in the Mississippi Valley in which lakes may be either dimictic or warm monomictic. Table 15 presents mean temperatures prevailing in this region during both winter and summer. These temperatures influence the thermal regimes of lakes in the region which roughly corresponds to the Zone of Statistical Overlap.

The significance of this relationship is difficult to envisage at this time, since work on the physiological ecology of the chydorids is lacking due to the absence of successful culturing techniques. The fact that a lake has a long season of open water can mean a greater number of chydorid generations during the year. Also, the warming of the water takes place more rapidly during the spring if an ice cover is absent. Hence, heat normally utilized in melting the ice would be immediately available for warming the water. This factor coupled with the higher summer temperatures results in a warmer habitat of longer duration than could be expected in a dimictic lake.

Summer temperatures might have a profound influence on the chydorid distribution. The temperatures of the littoral zone during the summer, where the chydorids live, have been known to be higher and fluctuate more than temperatures in the pelagic zone.

A recent important paper on the temperatures of the littoral zone of Polish lakes by Gieysztor (1960) demonstrates that: 1) the course of temperatures in the littoral zone differs considerably from that of the surface water of the open lake; 2) the character of littoral temperatures corresponds in general with the character of the thermal conditions of ponds; 3) the maximum 24-hour temperatures of the littoral during the

summer greatly exceed the maximum 24-hour temperatures of open water; 4) during late fall the temperatures of the littoral are in general slightly lower than temperatures of the open waters. Gieysztor concluded:

"It may be considered that the thermal character of the littoral may be very varied depending on development of its width, depth, on the extent to which it is isolated from the center of the lake or to which it is overshadowed, on its exposure to sunlight, its degree of turbulence or stagnancy, and finally the vegetation present. These wide possibilities for the formation of various types of littoral which affect its thermal character presents a large field of study of the thermal properties of this zone of a lake."

The summer temperatures in the Zone of Statistical Overlap appear to be those necessary from the viewpoint of climate to form a barrier for the colonization southward of strictly northern species and at the same time are not sufficiently high to permit large populations of southern chydorids to build up consistently year after year. Hence, the eurytopic forms are able to gain ascendancy in this zone.

The mean temperatures over the southern boundary of the Zone of Statistical Overlap are probably close to those that permit dominance of a southern fauna, for it is here that the southern species gradually begin to gain ascendancy throughout the Transition Zone.

DISCUSSION

In this study a quantitative approach has made it possible to describe the zonation of the chydorid fauna of the Mississippi Valley. The chydorids are seen to be zoned in accordance with general limnological conditions, which are reflections of broad climatic factors. The chief contribution of this study is the demonstration that micro aquatic organisms, using the chydorids as an example, do show subtle changes in response to changes in climate.

The dominance of eurytopic forms in the Zone of Statistical Overlap might indicate that they are pioneer species, since most lakes in this zone are artificial. However, these species still dominate in natural lakes of the zone, and in the Southern Zone newly formed lakes have faunas which are dominated by southern species.

Ueno (1938) studied the zoogeography of the Cladocera of Japan based on the collection of living animals. Although he admitted that most chydorids are eurytopic, his conclusions were similar to the conclusions of this study. The southward extension of the boreal species was restricted to lakes in which the temperature of the water was usually lower than 20° C in the summer. The northern limit of the austral species seemed roughly to correspond to the northern limit of the lakes whose surface temperature was usually higher than 4°C in winter (warm monomixis). These conclusions coincide nearly exactly with those of the present study.

It should be emphasized that the climatic gradients existing in the Mississippi Valley may not be duplicated in other sections of North America or at least are not equivalent latitudinally. The conclusions regarding the region of overlap as defined do not necessarily exist in other regions of North America, although in general the definition of the regional faunas may be found to apply. Although a great many lakes have been sampled via their living populations in four studies in western

North America, the only species reported fall into either the eurytopic or northern groups of this study (Carl, 1940; Dodds, 1919, 1920; Reed and Olive, 1958). Since these studies were not quantitative there was no method to differentiate the various life zones of the chydorids. Therefore it is not possible to compare the results of the current study with previous work where altitude is an important variable. Only studies based on sedimentary remains of chydorids could make it possible to make a strict comparison. Collections of living populations where southern species are found in the north and vice versa may not be accurate observations of the long term establishment of a species. Frey (1960) found species in the Madison lakes that had not been collected by Birge in his extensive collecting. Conversely he did not find *Dunhevedia crassa*—a southern species—in the sediments of a lake in which Birge found this species only once but then in large numbers. This lends weight to the conclusion that an occasional large population of a species may spring up during favorable conditions, where otherwise it may be found only fortuitously or not at all by collecting in the living populations.

Dice (1943) has defined the biotic provinces of North America. He states that the boundary between the Carolinian province and the Austroriparian province in the region of southern Illinois is difficult to determine. His main criteria for defining provinces are vegetation, birds, and mammals. The conclusions of this study show that the ill-defined boundary cited by Dice is justified. The chydorids in this region are dominated by eurytopic forms. Assuming that the chydorids are better indicators of climate conditions than are terrestrial organisms, then no definite boundary exists in the Mississippi Valley between the Carolinian and Austroriparian provinces. Rather a broad belt of gradual transition between the two provinces exists, and this belt is defined by the Zone of Statistical Overlap. This belt of transition between the two provinces seems to be a buffering zone between the two regional faunas of the chydorids. The Mississippi Valley is a corridor in the sense of Simpson (1953). Although he does not make this distinction, it can readily be seen that with constant introduction from both directions because of the lack of physical barriers, neither northern nor southern species can colonize their opposite zones.

The rapid colonization and subtle adjustments to climate that seem to characterize the chydorids make it likely that during the Pleistocene glaciations they did not remain in refugia along the ice margin. Considering the accumulating evidence of a southward shift of the climatic zones of North America (Reviews by: Dorf, 1960; Martin, 1958), it appears quite consistent with the conclusions of this study to suggest that the chydorid assemblages, too, shifted southward. However they no doubt colonized new habitats very quickly upon the retreat of the ice (Frey, 1962).

If this is true, then the importance to paleolimnology of the chydorids cannot be overemphasized. They may be sensitive enough to indicate a change from dimixis to intermittent dimixis and warm monomixis as chydorid spectra changed during lake ontogeny. The large abundance of chydorid remains in lake sediments makes such a statistical treatment possible.

IDENTIFICATION OF UNKNOWNNS

A number of remains not previously described in the literature have been found and identified during the course of this study. Most of these are from southern species.

Alona verrucosa Sars has not previously been reported from the United States. Frey (pers. comm.) found it commonly in lakes of southern Florida. The striking bulbous structures around the minor

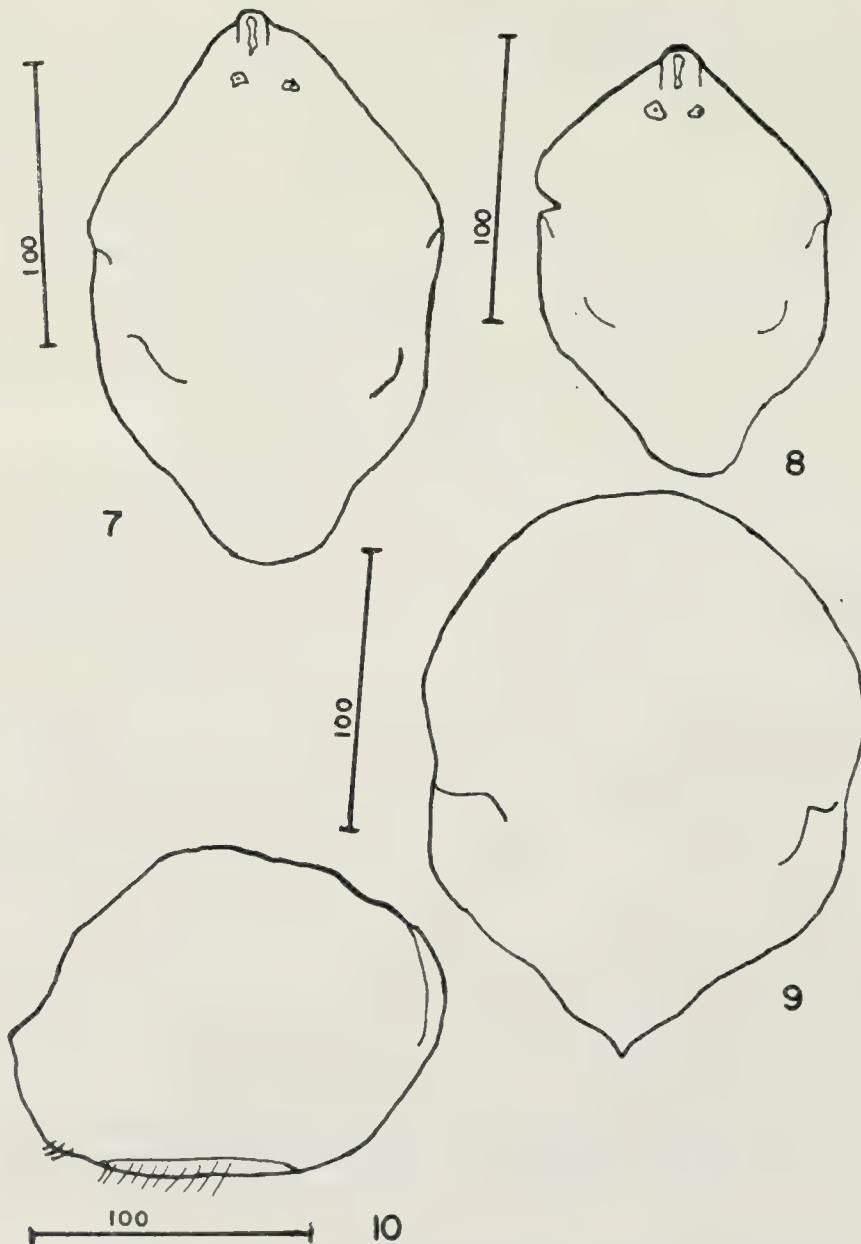


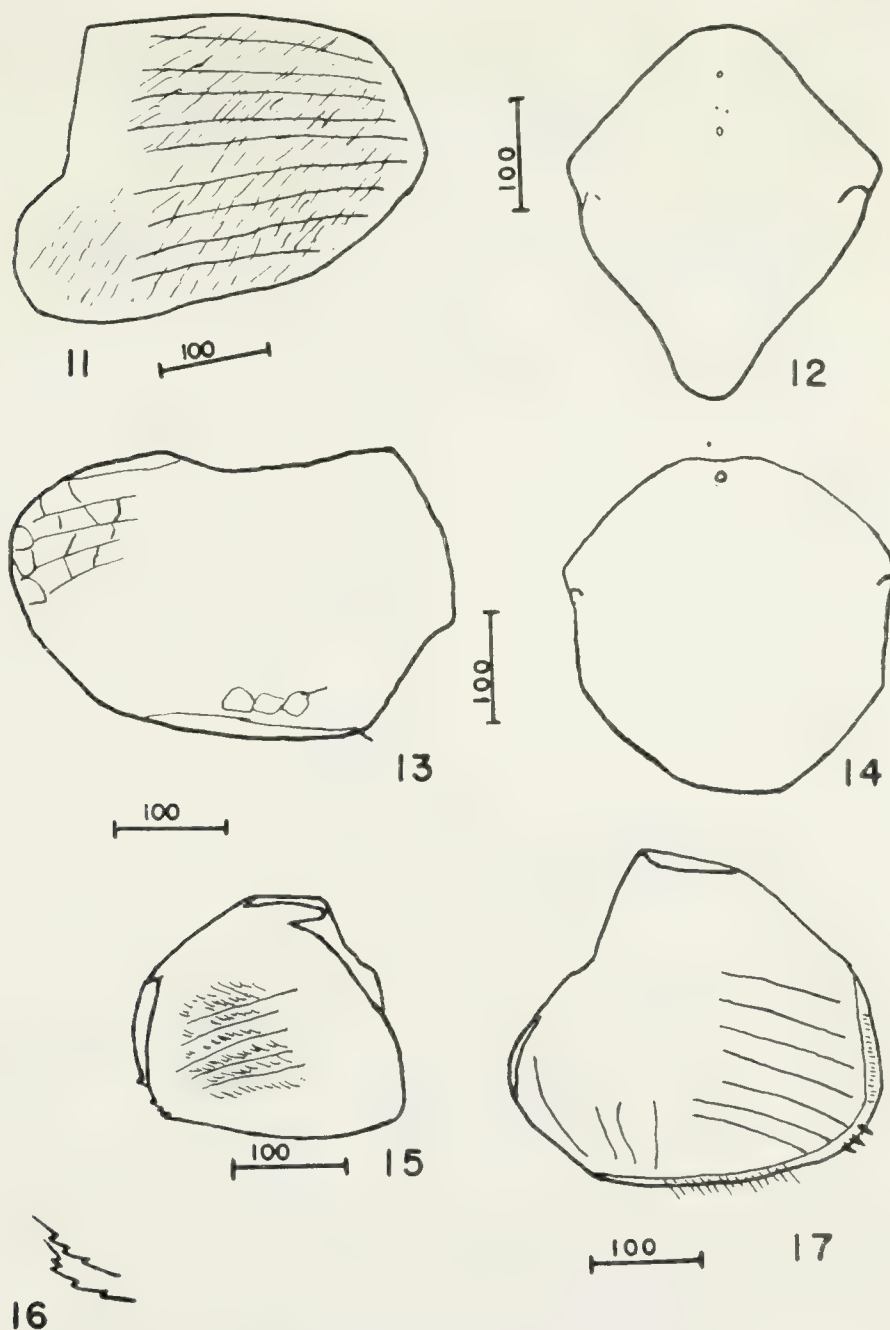
FIG. 7. *Alona verrucosa* ?, head shield. Lake Chicot, La.¹

FIG. 8. *Alona verrucosa* head shield. Dun-Roamin Lake, La.

FIG. 9. *Chydorus* sp., head shield. Lake Chicot, La.

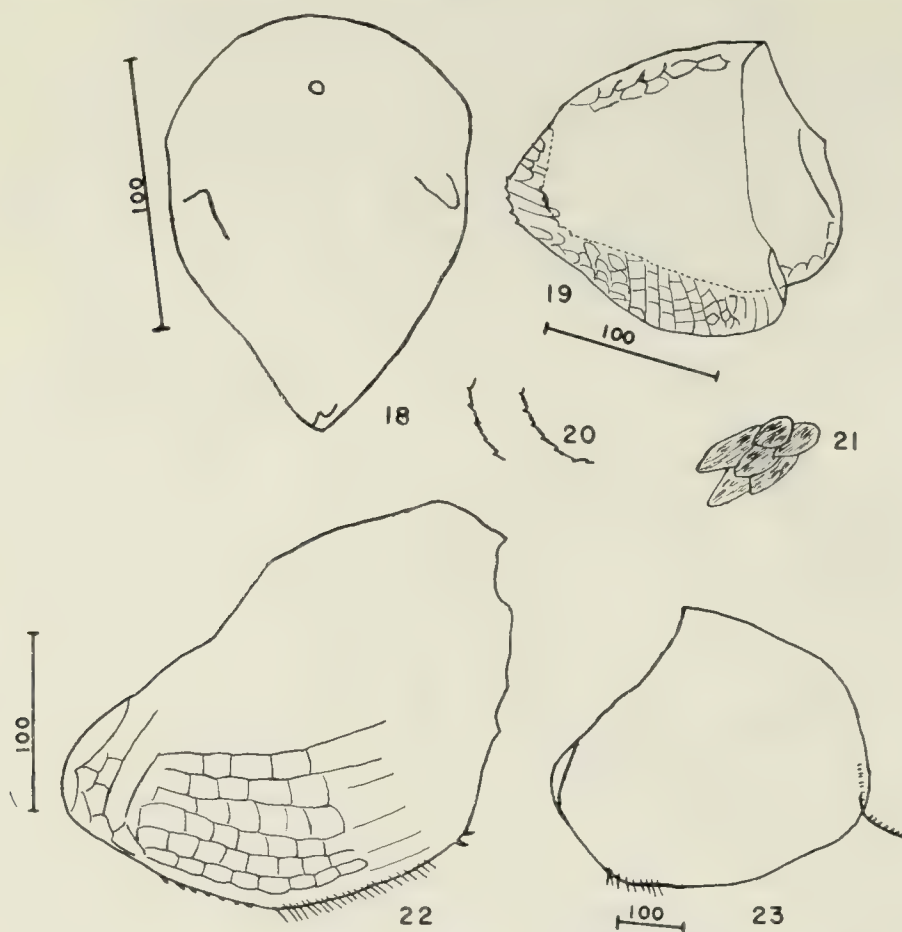
FIG. 10. *Chydorus* sp., shell. Lake Chicot, La.

¹ All figures of chydorid remains in Fig. 7-23 were drawn by means of camera lucida. Scales are in microns.



- FIG. 11. *Alonella hamulata*, shell. Lake Chicot, La.
 FIG. 12. *Dunhevedia serrata*, head shield. Lake Chicot, La.
 FIG. 13. *Chydorus* sp., shell. Cannon's Lake, La.
 FIG. 14. *Euryalona occidentalis*, head shield. Lake Concordia, La.
 FIG. 15. *Alona karua*, shell. Otter Pond, Ill.
 FIG. 16. *Alona karua*, detail of teeth of same shell. Otter Pond, Ill.
 FIG. 17. *Alonella globulosa*, shell. Otter Pond, Ill.

pores (Fig. 8) are clearly visible in intact specimens. The head shield in Figure 7 is larger than the typical *verrucosa* shield, and it also has a small anterior extension of the anterior major pore. In both head shields illustrated the minor pores are located in lobular areas that appear to be thin places in the shield.



- FIG. 18. Unknown head shield (*Dadaya macrops?*). Cannon's Lake, La.
 FIG. 19. *Alonella dadayi*, shell. Lake Chicot, La.
 FIG. 20. *Alonella dadayi*, detail of teeth of same shell. Lake Chicot, La.
 FIG. 21. *Alonella dadayi*, detail of same shell. Lake Chicot, La.
 FIG. 22. *Chydorus* sp., shell. Lake Chicot, La.
 FIG. 23. *Euryalona occidentalis*, shell. Lake Concordia, La.

The *Chydorus* spp. complex is represented here by four types of remains. The head shield in Figure 9 is typical in that at no time were pores found in any of these shields. Disarticulated specimens in the collection of D. G. Frey of *Chydorus hybridus* and *C. barroisi* revealed head shields identical to the one shown here. Living specimens from Cannon's Lake, Louisiana, had shields of this type. However, the specimens cannot yet be assigned to any known species of *Chydorus*.

The shells of this group (Fig. 10, 13, 22) are typical for the genus *Chydorus*, although they differ from each other in the armature at the inferoposteal angle. The armature varies from heavy hairs (Fig. 10, 13) to definite spines (Fig. 22). The number of these hairs or spines also varies. The inferoposteal angle of both *C. barroisi* and *C. hybridus* bears a spine, which *C. poppei* does not. Other distinguishing characteristics of the shells of these three species must be found before sedimentary remains of them can be properly identified.

Alonella hamulata remains have not been previously figured in the literature. The shell in Figure 11 is typical. It closely resembles

Alonella acutirostris (Frey, 1961) in shape, but the coarse longitudinal striae do not form closed cells, and the cross-hatched appearance of the *hamulata* shell is due to the crossing of the coarse striae by fine scratch marks as shown here and revealed on examination of any specimen under high power.

A head shield now assigned to *Dunhevedia serrata* is shown in Figure 12. It differs from *D. crassa* head shields by having lateral bulges anterior to the major pores. Otherwise it is quite similar to *crassa*. The shells of the two species are nearly identical except that *crassa* always has only one inferoposteal spine, whereas *serrata* typically possesses two but may show only one. Other characteristics must be sought to differentiate these one-spined *serrata* from those of *crassa*.

Euryalona occidentalis (Fig. 14) possesses a head shield with only one large pore. The shape of the shield is distinctive. The shell of *Euryalona* (Fig. 23) is reminiscent of the larger Alonas. It differs from them in possessing no striae or scratch marks of any sort, and it shows a bulge anteroventrally caused by the gaping of the anterior portion of the valves.

The head shield of *Alona karua* was figured by Frey (1959). The shell shown here (Fig. 15) is typical. The number of spines at the inferoposteal angle is variable, and may even differ on the two sides of the same specimen (Fig. 16). The coarse striae have very fine scratch marks running obliquely to them, which however do not cross the long striae.

The *Alonella globulosa* shell shown in Figure 17 shows three fairly strong spines at the inferoposteal angle. The shell shown here is not typical for the genus *Alonella*, and neither is the head shield which is figured by Mueller (1964). Eventually this species may have to be placed in a separate genus.

Figure 18 shows a head shield which at present is unidentified. Possibly it is from *Dadaya macrops*, but good reference preparations of this species are not available.

The shell of *Alonella dadayi* (Fig. 19-21) has not been figured previously in the literature. The shell is typical in shape and reticulation pattern for the genus. The inferoposteal angle armature consists of 3-4 small teeth between each large one. The closed cells of the shell reticulation have fine scratch marks within them.

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Further Studies on the Metalimnetic Oxygen Maximum, with Special Reference to Its Occurrence Throughout the World

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ABSTRACT

Lake water can be saturated with oxygen largely through physical means during the period of spring circulation. At the hypothetical homothermous temperature of 4° oxygen saturation occurs at 12.7 mg/L (at sea level). It is suggested that the oxygen content of the metalimnion should exceed this value before the term "plus-heterograde" is applicable to the resulting oxygen curve. A lake that exhibits a plus-heterograde oxygen curve throughout most of the period of summer stagnation until the beginning of fall circulation is called a *plus-heterograde lake type*.

A list of 54 lakes from various areas of the world has been compiled, from which 98 separate instances of metalimnetic oxygen maxima (in some cases representing several years) have been observed. Most of these lakes occur in the glacial region of Wisconsin and Indiana, the Alpine mountains of Switzerland and Austria, and the mountain regions of Japan. Morphometry (both area and relative depth) appears to be a significant factor in the development of the metalimnetic oxygen maximum in the US lakes. Variations in the oxygen maximum could be related to area in the Japanese lakes but not to relative depth. No positive correlation between any morphometric character and the oxygen maximum seemed to exist in the Alpine lakes.

Four types of oxygen maxima are described. The *pseudo-metalimnetic oxygen maximum* develops temporarily early in the summer under a high secondary thermocline in very small, well protected lakes. A *temporary sub-climax oxygen maximum*, with highest values in early summer, occurs in the deep layers of the metalimnia of lakes with high transparency. *Permanent climax oxygen maxima* are characteristic throughout most of the summer and generally reach highest oxygen values just prior to the beginning of fall circulation. Two sub-types, *Diatom maxima* and *Oscillatoria maxima*, are differentiated on the basis of the dominant phytoplankton organisms present.

Primary production in Myers and McLish lakes, two *Oscillatoria*-lakes in northern Indiana, is discussed. Photosynthetic efficiency in the metalimnion at the level of maximum oxygen production is approximately 0.8% in McLish Lake and 1.7% in Myers Lake. Overall production in McLish is about 0.7 g C/m²/day and in Myers during the time the extensive plankton bloom was present about 1.7 g C/m²/day (late summer rates). Very little bacterial and/or nannoplankton activity seems to be evident at the levels of maximum *Oscillatoria* population.

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INTRODUCTION

The presence of excessively large amounts of dissolved oxygen in the metalimnion of lakes has been noted many times. Probably the earliest account was that of Birge and Juday (1911), who reported oxygen concentrations of 36.5 mg/L at 4.5 m in Knights Lake and 35.7 mg/L at 4.5 in Otter Lake, both in central Wisconsin. Lesser maxima were noted for several other Wisconsin lakes then as well as in a later paper (Juday and Birge, 1932).

Deep water oxygen maxima in Indiana lakes were noted by Scott (1931) and Frey (1955a). The metalimnetic oxygen maximum in Myers Lake was studied extensively from 1951 to 1955 (Eberly, 1959). The most pronounced oxygen maximum in any Indiana lake has been observed in McLish Lake where 33.2 mg/L was found at 6 m on one occasion (Eberly, 1964 in press). Oxygen production in some Indiana lakes, with special reference to those with metalimnetic oxygen maxima, has been discussed by Eberly (1963).

Outside the United States metalimnetic oxygen maxima have been observed chiefly in some of the lakes of Japan (Yoshimura, 1938) and in the Alpine lakes of Switzerland and Austria. Other isolated examples are known from Poland and the USSR. The present paper is a further effort to define the metalimnetic oxygen maximum as a biogenic phenomenon and to discuss the relation of this particular type of oxygen distribution to lake morphometry and lake typology in general. A listing of the known cases of high metalimnetic oxygen concentrations in lakes of the world is presented, and various analyses are made to determine what, if any, causative relationships may be deduced from morphometry, lake stability, etc. A classification of four types of metalimnetic oxygen maxima is suggested along with a discussion of primary production in "*Oscillatoria* lakes" that are characterized by the plus-heterograde type of oxygen profile.

THE PLUS-HETEROGRADE LAKE TYPE

Efforts to classify lakes have been made by many limnologists using many and varied parameters and characteristics. No attempt is made here to summarize the various schemes that have been advanced, as such reviews are already rather numerous (e.g., see Elster, 1958). There appears to be general agreement that the trophic nature of the lake should be the most basic character in classification rather than such factors as size, morphometry, etc. Since the production and consumption of oxygen is involved in much of the internal metabolism of a lake, the quantity and distribution of dissolved oxygen present at a given time has often been used as an indicator of the trophic level of the lake and consequently has served as a basis for classification.

In considering lake typology it must be remembered, as Gieysztoř (1959) has so well pointed out, that lakes do not exist in discontinuous categories but as continuous series. No matter how well-defined a certain character may seem when applied to a particular group of lakes, these lakes are always related to other groups of lakes of an intermediate character. The widely accepted oligotrophy-eutrophy scheme has a great deal of validity even though precise quantitative limits for each category have by no means been agreed upon. Rather than to define the trophic level of a lake in terms of the quantification of some of the factors that influence productivity (e.g., range of concentration of some nutrient substance or some morphometric character), a measure of the actual production would seem to integrate the effectiveness of all factors relative to productivity. In all likelihood, measurements of primary production will prove to be most useful in this connection (Rodhe, 1958).

The introduction of terms that indicate intermediate levels of productivity is rejected by some workers, while others erect a great number of graduated types. The use of a single intermediate category, mesotrophy, seems justified for several reasons. Probably the great majority of lakes will be found to be of moderate productivity. In fact, mesotrophy might be defined in terms of the median range of productivity. Furthermore, by distinguishing the majority of lakes as mesotrophic, added emphasis is given to conditions of low (oligotrophy) and high (eutrophy) productivity. Of 148 "normal" lakes in Japan, Yoshimura (1938) classified 64 (43%) as mesotrophic, 47 (32%) as oligotrophic, and 37 (25%) as eutrophic.

The oxygen curve nomenclature proposed by Åberg and Rodhe (1942) is widely accepted. An orthograde oxygen curve is defined by having some oxygen present to the bottom of the lake, while a clinograde curve is always characterized by the absence of oxygen in the hypolimnion. Levels of maximum or minimum oxygen concentrations can occur in the metalimnion, the former termed plus-heterograde and the latter minus-heterograde.

During the period of spring circulation, water can be uniformly saturated through surface aeration and turbulent distribution. At 4° C, the saturation value is 12.7 mg/L (Truesdale *et al.*, 1955). In the absence of pronounced metabolic activity in the intermediate strata of the lake, oxygen concentrations can remain at or near the spring saturation level for some time, although the increase in temperature creates a super-

saturation. Consequently, when the hypolimnetic oxygen is consumed by decomposition and respiration and the epilimnetic oxygen is reduced through contact with the atmosphere, a plus-heterograde curve can result. Because there is such a wide range of intermediates between the plus-heterograde curve and the orthograde and clinograde curves and because of the possibility of physically induced oxygen entering into a determination of the oxygen profile, a redefinition of the plus-heterograde curve is suggested (Eberly, 1963).

Since 12.7 mg/L is the maximum concentration of oxygen that can be present in summer through purely physical means, it is reasonable to require that oxygen values in the metalimnion must exceed saturation of 4° before the term plus-heterograde is appropriate. Because the saturation of oxygen is affected by atmospheric pressure, the actual prestratification saturation value for all lakes except those at or near sea level will be somewhat less than 12.7 mg/L. In general, a correction for altitude is sufficient to compensate for pressure differences (Mortimer, 1956). Oxygen in excess of the spring saturation value definitely indicates photosynthetic activity in the metalimnion.

Usually dimictic lakes of the temperature region emerge from the winter period with rather uniform oxygen concentrations from surface to bottom, a typical orthograde curve. As the summer progresses, this curve is often replaced by one or more of the other types of curves. In general, the trend is toward a clinograde curve as a summer climax. In a highly oligotrophic lake, an orthograde curve is maintained throughout the summer, with often a slight reduction of oxygen at the bottom. Strongly eutrophic lakes early develop a clinograde curve directly from the spring orthograde pattern.

The more mesotrophic lakes exhibit a variety of summer successional patterns, sometimes including a plus-heterograde curve temporarily early in the summer or as a permanent summer climax. In nearly every case the metalimnetic oxygen maximum develops before the hypolimnetic oxygen disappears. When the maximum exceeds 12.7 mg/L (or equivalent value corrected for altitude), the plus-heterograde curve results. If the level of production in the metalimnion decreases and the oxygen level falls below the prestratification saturation value, the plus-heterograde curve regresses to an orthograde curve or develops into a clinograde curve, depending on whether there is any oxygen left at the bottom. Minus-heterograde curves seem to be closely related to clinograde curves in their successional patterns. These suggested relationships are shown schematically in Figure 1. Besides representing seasonal relationships, this scheme can also indicate the succession of oxygen types in the evolution or life history of a lake. In this connection the trophic levels they represent are more significant than the oxygen curves themselves.

All of the metabolic activities of the lake that affect the oxygen profile reach a climax toward the end of the period of summer stratification. Therefore, oxygen curves that are intended to type lakes should be taken during this period, preferably during August or early September in the north temperature region. Evidence of the beginning of fall circulation may appear earlier in lakes of high altitude or high latitude. An oxygen curve that shows no further change, typologically, until the beginning of

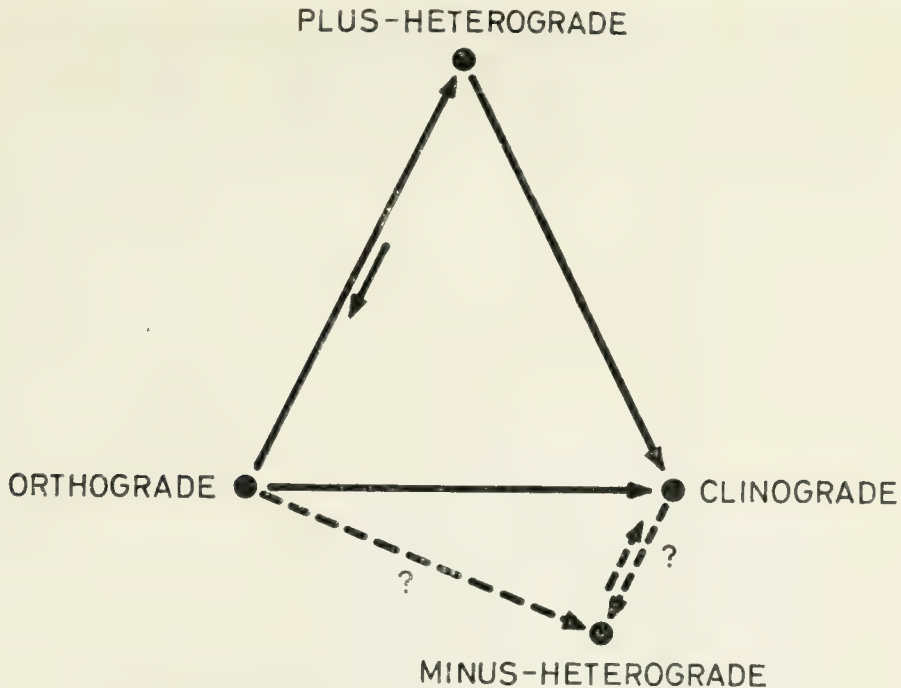


FIG. 1. Possible successional relationships of major types of oxygen curves.

the fall circulation period is the summer climax type. A *plus-heterograde lake* is defined simply as a lake that develops a plus-heterograde oxygen curve as a summer climax type of oxygen distribution. Plus-heterograde curves that develop temporarily at other times of the year will be considered later.

As indicated previously the orthograde curve is associated with oligotrophic lakes, while the clinograde curve indicates eutrophy. It is the opinion of the writer that most lakes with the plus-heterograde oxygen curve are mesotrophic. Three such lakes in Indiana (Myers, McLish, and Taylor) are known to have daily summer production rates ranging from 0.7 to 1.8 g C/m². Yoshimura (1938) considered 8 of the 12 Japanese lakes with plus-heterograde curves included in this study to be mesotrophic. Several of the Alpine lakes have been considered by various authors to be mesotrophic (e.g., Findenegg, 1963). Preliminary investigations in 7 of these lakes indicate daily production rates between 0.1 and 1.2 g C/m² Rodhe, unpublished data).

It is instructive at this point to examine a plus-heterograde oxygen curve in more detail. For this purpose a profile from McLish Lake (northern Indiana) on 25 August 1961 has been chosen (Fig. 2). On this date the oxygen maximum was 31.2 mg/L at 6 m. At this depth the light intensity ($I_{\%}$) was 2-3% of the surface illumination (measured with a Whitney underwater photometer without color filters), and the temperature was 13.8° C. Oxygen saturation values at the observed temperatures ($[O_2]_s$) are taken from the TDL table (Truesdale *et al.*, 1955; also in Hutchinson, 1957) and are corrected for altitude (Mortimer, 1956). The correction is made by multiplying the values in the table by the reciprocal of the factor given in Mortimer's nomograph. At an altitude of ca. 250 m, saturation values in McLish Lake are 3.5% lower than the

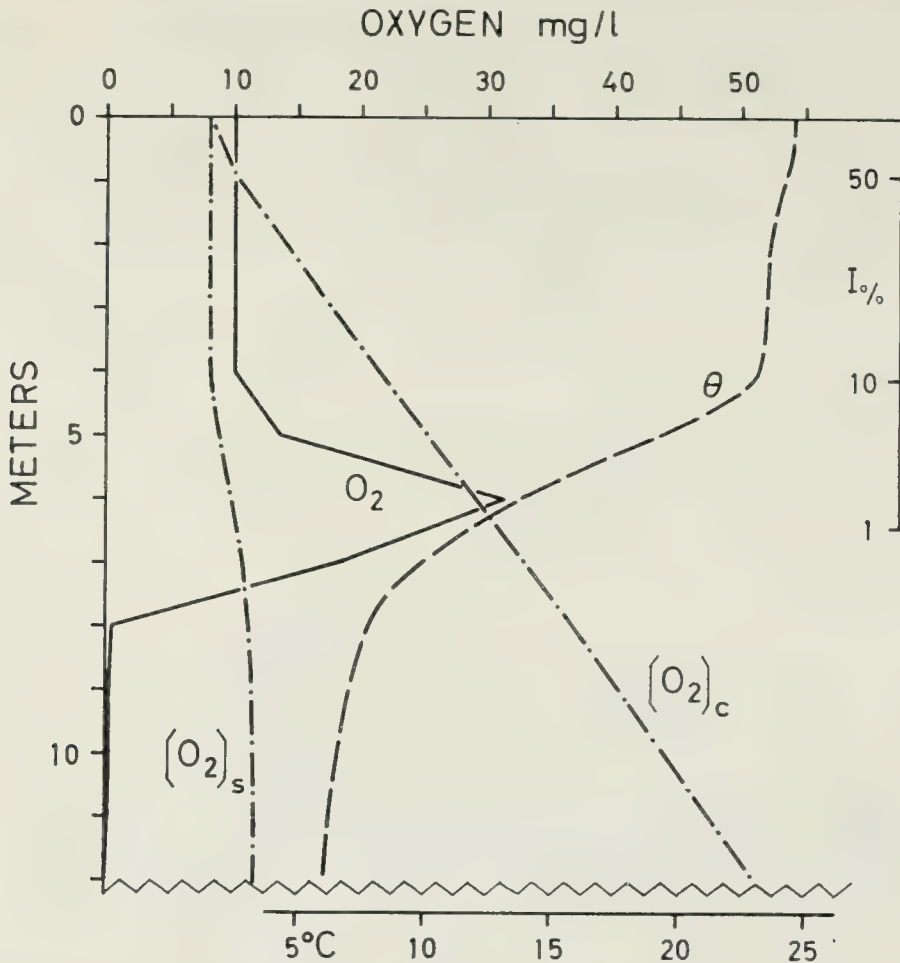


FIG. 2. Plus-heterograde oxygen profile from McLish Lake on 25 August 1961.
 θ = temperature distribution; O_2 = oxygen concentration in ppm;
 $[O_2]_s$ = oxygen saturation at observed temperature, corrected for altitude;
 $[O_2]_c$ = absolute saturation based on hydrostatic pressure.

values at sea level. The epilimnion is rather uniformly supersaturated at about 125%. During periods of relative calm, epilimnetic oxygen concentrations often exceed saturation levels, because the oxygen is produced more rapidly than the slowly circulating water mass can be brought into equilibrium with the atmosphere. This is not unusual in small, well protected lakes. McLish Lake (13.7 ha) is surrounded by trees and hills, which shield it from extreme effects of the wind.

The saturation at 6 m where the maximum occurred was 323%. On 15 August 1961 a maximum of 33.2 mg/L was recorded, also at 6 m, which was 340% saturation. The maximum concentration observed by Birge and Juday (1911) in Knights Lake was 36.5 mg/L at 4.5 m, a saturation of 385%. The maximum concentration in Otter Lake, 35.7 mg/L, represents a saturation of about 415% (a temperature of 19.7° was calculated from the saturation table given by Birge and Juday).

The concept of absolute saturation (Ricker, 1934; Hutchinson, 1957) incorporates the additional effect of hydrostatic pressure on the solubility of oxygen. Absolute saturation is the minimum concentration of oxygen, relative to surface saturation, necessary for the formation of bubbles of

free oxygen. These values ($[O_2]_c$) are calculated for each depth z from the equation given by Hutchinson (1957).

$$[O_2]_c = [O_2]_s (1 - 4.78 p_w - 0.462 z)$$

where $[O_2]_s$ is the surface saturation value (corrected for altitude) and p_w is the pressure (in atmospheres) of water vapor at the temperature existing at depth z .

The oxygen maximum at 6 meters exceeds the "bubbling point" (29.1 mg/L) by about 7%. The earlier value of 33.2 mg/L is 117% absolute saturation (28.4 mg/L). The highest concentration in Knights Lake represents about 150% absolute saturation, and the maximum concentration in Otter Lake, based on an estimated surface temperature of 26°, is about 156% absolute saturation.

The formation of bubbles depends on the presence of quantities of the free gas that can act as nuclei. In the absence of such free oxygen, an enormous degree of supersaturation is necessary in order for bubbles to form spontaneously when the pressure is reduced (see Hutchinson, 1957; footnote p. 583). Some bubble formation, almost like effervescence, has been noted at times when such highly saturated water is brought to the surface. But to the writer's knowledge no one has observed the *in situ* production of oxygen bubbles in undisturbed deep-water strata super-saturated with oxygen. Presumably if bubbles did form and begin to rise toward the surface, they would be reabsorbed by passage through the under-saturated upper layers. Such bubbles would be very small, since they would begin to rise as soon as they were formed. Furthermore, because the super-saturated strata are usually very thin, the bubbles would not remain long in the layer where they could accumulate more oxygen. On the contrary, quite large bubbles can readily be observed during active photosynthesis by certain vascular plants, such as *Vallisneria* and *Elodea*. Here the intercellular accumulation of oxygen before bubbles are erupted from the plant surface is quite a different mechanism from the diffusion of oxygen through the cell membrane of phytoplankton.

METALIMNETIC OXYGEN MAXIMA IN LAKES OF THE WORLD

In routine limnological surveys, metalimnetic oxygen maxima may be overlooked for several reasons. The common practice of taking oxygen measurements at large depth-intervals can easily miss the strata with high oxygen concentrations, which may be less than 2 m thick. Again, since some lakes develop maxima that persist for a relatively brief period of time, sporadic or infrequent sampling may not detect the greatest accumulation of oxygen. Some maxima form in late spring or early summer and disappear when the sinking metalimnion incorporates the oxygen-rich stratum into the epilimnion. Finally, the most pronounced maxima are more likely to be found in small lakes, which have been relatively neglected in limnological work. In the glacial lake district of North America are many small lakes for which little or no limnological data are available. Further study will undoubtedly show that the metalimnetic oxygen maximum is a far more common phenomenon than is now thought.

From a study of the literature as well as from some unpublished data, a list has been compiled of 54 lakes in which metalimnetic oxygen maxima

TABLE 1. Morphometric data on lakes with metalimnetic oxygen maxima, arranged in order of increasing z_r . Locality abbreviations: Austria (A), Germany (G), Indiana (I), Japan (J), Poland (P), Russia (R), Switzerland (S), Wisconsin (W).

A = area; z_m = maximum depth; \bar{z} = mean depth; z_r = relative depth; Alt. = altitude.

Lake	A <i>ha</i>	z_m <i>m</i>	\bar{z} <i>m</i>	\bar{z}/z_m	z_r <i>%</i>	Alt. <i>m</i>
Clear (W)	418.	29.3	8.8	0.30	1.28	500
Hallwilersee (S)	1029.	47.	20.6	0.43	1.29	452
Black Oak (W)	230.	26.	10.3	0.40	1.52	500
Zürichsee (S)	6848.	143.	44.	0.31	1.53	409
Clear (I)	310.	32.			1.62	260
Gage (I)	132.	21.3			1.65	260
Wörthersee (A)	1940.	84.	43.	0.51	1.68	500
Faaker See (A)	235.	30.	14.3	0.48	1.73	500
Silver (W)	87.3	19.5	11.3	0.58	1.85	500
Rotsee (S)	47.5	14.5			1.86	423
Palette (W)	68.6	18.0	9.7	0.54	1.98	500
Sempachersee (S)	1410.	87.	46.	0.53	2.05	507
Längsee (A)	76.	21.	11.2	0.53	2.13	548
Hindman (I)	6.1	6.0			2.16	240
Taylor (I)	6.9	6.6			2.23	250
Pleasant (I)	19.4	12.			2.41	260
Baldeggersee (S)	523.	66.	34.	0.52	2.55	450
Schleinsee (G)	14.9	11.6	6.4	0.55	2.66	475
Gordy (I)	11.5	10.5			2.76	240
Cook (I)	23.1	15.			2.76	230
Elkhart (W)	121.2	34.5	13.5	0.39	2.78	250
Türlensee (S)	48.	22.	14.0	0.64	2.81	450
Hüttnersee (S)	16.	13.			2.88	450
Myers (west) (I)	28.8	17.9	6.9	0.39	2.94	234
Wyland (I)	3.2	6.3	3.9	0.62	3.11	250
Long (W)	43.9	23.7	9.9	0.42	3.18	244
Garvin (W)	8.8	11.0	5.0	0.45	3.29	250
Crooked (I)	77.7	33.			3.33	250
Millstätter See (A)	1330.	141.	86.	0.61	3.42	580
Rainbow (W)	55.7	29.	11.2	0.39	3.45	244
Anderson (W)	21.	19.5			3.77	500
Klopeiner See (A)	113.	46.	25.9	0.56	3.82	500
Otter (W)	5.8	10.7	3.8	0.36	3.94	244
Knights (W)	8.5	13.0	4.7	0.36	3.96	244
McLish (I)	13.7	17.4	10.2	0.59	4.16	250
Still (I)	12.1	17.7	6.3	0.36	4.53	260
Shikaribetsu-ko (J)	350.	99.	57.1	0.58	4.68	797
Tsuta-numa (J)	8.	15.7	6.3	0.40	4.91	450
Beasley (W)	5.8	14.0	7.2	0.51	5.16	244
Hancza (P)	300.	108.	41.	0.38	5.51	
Marl (W)	8.5	18.5	5.4	0.29	5.64	244
Maru-numa (J)	45.	47.	31.1	0.66	6.21	1403
Waku-ike (J)	2.3	10.8	7.0	0.65	6.30	580
Pipurger See (A)	13.4	27.			6.52	475
Hangetsu-ko (J)	4.5	18.2	4.4	0.24	7.60	270
Sumiyoshi-ike (J)	13.	31.5	23.1	0.73	7.75	38
S. O-ike (J)	9.	27.3	12.2	0.45	8.05	233
Shin-numa (J)	6.	23.2	8.3	0.36	8.36	415
N. O-ike (J)	5.4	24.	10.7	0.45	9.16	195
O-numa (J)	7.5	29.	10.4	0.36	9.34	410
Ketoba-no-ike (J)	4.	21.9	10.6	0.48	9.68	243
Finstersee (S)	3.	20.			10.21	500
Ochikuchi-no-ike (J)	3.	20.3	10.0	0.49	10.37	213
Belowod See (R)	3.	23.			11.76	
mean	298.8	32.1		0.47	4.30	
median	20.2	21.6			3.31	

greater than 12.7 mg/L have been observed (Table 1). The list includes 12 lakes from Indiana, 13 from Wisconsin, 14 from the Austrian and Swiss Alps, 12 from Japan, and one each from Germany, Poland, and Russia. No claim is made that the list is complete, even as far as the published data are concerned, but it is sufficient to permit some comparative analyses on a regional basis.

Maximum oxygen values observed in a given year along with temperature and saturation values are presented in Table 2. Some lakes are represented by data from as many as 9 years. Altogether 98 measurements are given. Some of the data for the European lakes were published as graphs or curves from which the values for oxygen concentrations and temperature in the table were approximated. Where data permitted, saturation values were computed and corrected for altitude as discussed earlier.

All of the lakes from northern Indiana are glacial ice-block lakes occurring in the prominent interlobate moraines of the area. Myers and Cook are in the "Twin Lakes Chain" in Marshall County about 4 miles southwest of Plymouth in the Maxinkuckee moraine. The rest are in the Packerton moraine in Kosciusko (Wyland), Whitley (Crooked), Noble (Gordy, Hindman), Lagrange (Taylor, Still), and Steuben (Clear, Gage, Pleasant, McLish) counties. With the exception of Gordy and Hindman, which are in the "Indian Village" chain, none of the others are associated in any group or chain. General information about Indiana lakes can be found in Bechtol (1955).

The Wisconsin lakes are also glacial in origin. Knights, Otter, Beasley, Marl, Long, and Rainbow are part of the "Waupaca Chain of Lakes" near the city of Waupaca in central Wisconsin. Elkhart is in Sheboygan County and Garvin is in Waukesha County, both in southeastern Wisconsin. The rest are in the Highland Lake district in northeastern Wisconsin (Juday and Birge, 1941). General data on Wisconsin lakes can be found in Fenneman (1902) and Juday (1914).

Zürichsee, Türlensee, Hüttnersee, Finstersee, Baldeggersee, Hallwilersee, Rotsee, and Sempachersee are in the Swiss Alps in the vicinity of Zürich. Millstätter See, Klopeiner See, Wörthersee, Längsee and Faaker See are in the Carinthian lake district of southeastern Austria. The first four are meromictic (see Frey, 1955b). Schleinsee is in southern Germany, and Pipurger See is in western Austria.

Little information about Hancza and Belowod-See is available. A summary of the limnological characteristics of Hancza is presented by Szezepanski (1961), but the original data on the oxygen maximum are from Kozminski (1932). Other oxygen maxima in Polish lakes (Czeczuga, 1959) are not included in the present study, because the oxygen concentrations were less than 12.7 mg/L. Kuznetsov (1959) mentions two lakes in Russia with high concentrations in the metalimnion, Beloje-See (*ca.* 12 mg/L at 3 m) and Belowod-See (14.2 mg/L at 5 m). Of these lakes he says only that they have a surface area of 2-3 ha and are located in a wooded region. Lake Byelovod (Kuznetsov, 1958) appears to be identical with Belowod-See and is included under the latter name.

Descriptive data as well as the spelling of the names of the Japanese lakes are from Horie (1962). The 12 lakes included in this study appear

TABLE 2. Metalimnetic oxygen maxima greater than 12.7 mg/L, arranged in order of decreasing oxygen content. Only the highest maximum observed in a given year for each lake is listed. Depth of oxygen maximum in meters (z), temperature at depth of oxygen maximum (t), saturation at observed temperature (S), absolute saturation (S_a).

Lake	Date	O ₂ mg/L	z m	t °C	S %	S_a %	Reference
Knights	26.8.09	36.5	4.5	15.1	385	152	Birge & Juday, 1911
Otter	25.7.10	35.8	4.5	19.7	416	156	Birge & Juday, 1911
McLish	15.8.61	33.2	6.0	13.2	340	128	Eberly, 1964
Hallwilersee	23.9.42	29.4	10.	21.	359	65	Jaag, 1949
McLish	17.7.62	28.9	6.0	14.0	300	98	Eberly, 1964
Otter	26.8.09	27.0	4.0	19.3	312	127	Birge & Juday, 1911
Zürichsee	11.9.47	27.0	10.	18.	309	60	Thomas & Märki, 1949
Myers	7.9.53	23.3	8.0	12.1	230	64	Eberly, 1959
Zürichsee	14.8.45	23.0	12.	13.	239	43	Thomas & Märki, 1949
Hangetsu-ko	31.7.28	22.4	3.0	21.1	268	129	Yoshimura, 1938
Myers	28.8.52	21.9	8.0	11.3	213	62	Eberly, 1959
Beasley	3.8.08	21.9	5.0	19.1	252	88	Birge & Juday, 1911
Otter	20.8.06	21.6	3.5	21.	257	114	Birge & Juday, 1911
Otter	3.8.08	20.4	4.0	16.5	223	98	Birge & Juday, 1911
Zürichsee	June.21	20.4	10.				Minder, 1926
McLish	9.7.53	20.1	6.0	10.9	191	70	Eberly, unpublished
Türlersee	14.8.53	20.0	5.				Thomas, 1956
Marl	24.8.06	20.0	4.0	22.2	244	93	Birge & Juday, 1911
Zürichsee	22.7.49	20.0	9.	13.5	208	50	Thomas, 1957
Rotsee	10.6.58	19.7	2.	20.	235	135	Ambühl, 1958
Finstersee	17.7.47	19.7	5.				Thomas, 1949
Marl	6.8.59	19.4	5.0	19.5	225	80	Eberly, unpublished
Garvin	21.7.09	19.4	5.0	14.5	203	75	Birge & Juday, 1911
Wyland	11.7.55	19.3	2.0	25.0	246	148	Eberly, 1959
Myers	13.8.51	19.2	8.0	11.6	188	53	ILSS, unpublished
Türlersee	21.5.43	18.9	5.	10.	185	68	Thomas, 1948
Türlersee	21.7.52	18.3	5.				Thomas, 1956
Waku-ike	21.7.33	18.1	1.5	25.1	238	169	Yoshimura, 1938
Rainbow	16.7.09	18.0	7.0	13.2	184	55	Birge & Juday, 1911
Zürichsee	9.7.41	17.9	10.	12.3	182	42	Minder, 1943
N. O-ike	12.8.33	17.9	5.	13.7	183	73	Yoshimura, 1938
Marl	14.8.09	17.9	5.0	17.5	200	69	Birge & Juday, 1911
Knights	28.7.59	17.4	4.0	18.1	196	87	Eberly, unpublished
McLish	18.8.60	17.2	5.0	13.5	177	67	Eberly, 1964
Hindman	26.7.52	17.1	3.0	20.7	203	98	ILSS, unpublished
Taylor	8.7.60	17.0	3.0	18.3	193	93	Eberly, unpublished
Myers	26.8.54	17.0	8.0	11.0	164	48	Eberly, 1959
Hindman	29.6.53	16.9	3.0	22.3	206	102	ILSS, unpublished
Hüttnersee	17.7.47	16.9	2.5				Thomas, 1949
Myers	13.7.55	16.8	8.0	9.5	157	48	Eberly, 1959
Belowod-See	10.7.54	16.8	5.	12.8			Kuznetsov, 1958
McLish	15.9.52	16.7	6.0	12.9	170	56	Eberly, 1964
Ketoba-no-ike	11.8.33	16.2	5.0	14.3	169	60	Yoshimura, 1938
Ochikuchi-no-ike	11.8.33	16.2	5.0	14.3	169	63	Yoshimura, 1938
Beasley	16.7.09	16.0	5.0	15.4	171	61	Birge & Juday, 1911
Gage	6.7.29	16.0	8.				Scott, 1931
Zürichsee	20.8.46	16.0	8.	18.	184	42	Thomas & Märki, 1949
Beasley	16.8.05	15.9	6.0	12.8	161	53	Birge & Juday, 1911
S. O-ike	1.8.34	15.7	5.0	12.1	150	61	Yoshimura, 1938
S. O-ike	13.8.33	15.6	5.0	16.1	174	62	Yoshimura, 1938
Wörthersee	20.8.63	15.5	8.0	21.6	193	60	Findenegg, unpublished

TABLE 2. Continued.

Lake	Date	O ₂ mg/L	z m	t °C	S %	S _n %	Reference
Marl	23.6.07	15.5	5.0	11.9	153	58	Birge & Juday, 1911
Beasley	27.7.59	15.3	5.0	17.6	171	62	Eberly, unpublished
Längsee	15.9.35	15.0	10.	8.	185	32	Findenegg, 1947
Schleinsee	29.4.32	15.0	4.0	11.0	163	66	Klein, 1938
Silver	21.8.07	14.9	7.0	15.6	165	43	Birge & Juday, 1911
Zürichsee	15.5.17	14.9	10.	6.1	130	28	Minder, 1924
Still	21.6.61	14.8	7.0	10.0	140	41	Eberly, unpublished
Silver	9.8.09	14.7	7.0	10.1	144	45	Birge & Juday, 1911
Clear	11.8.09	14.7	8.0	11.4	143	39	Birge & Juday, 1911
Beasley	24.5.07	14.7	5.0	9.5	137	47	Birge & Juday, 1911
Long	16.7.09	14.7	5.0	17.0	162	59	Birge & Juday, 1911
Millstätter See	20.7.58	14.7	10.	12.8	153	33	Knie, 1958
Baldeggersee	8.6.58	14.6	4.0	16.5	165	64	Ambühl, 1958
Otter	2.8.59	14.5	4.0	18.0	163	69	Eberly, unpublished
Shin-numa	22.7.35	14.5	5.0	11.0	144	55	Yoshimura, 1938
Shikaribetsu-ko	9.8.37	14.4	12.	7.2	135	28	Yoshimura, 1938
Maru-numa	31.7.33	14.3	5.0	11.0	160	61	Yoshimura, 1938
Anderson	8.8.29	14.2	8.	10.	139	38	Juday & Birge, 1932
Belowod-See	30.7.38	14.2	5.	19.			Kuznetsov, 1959
Hallwilersee	7.9.58	14.2	3.5	22.5	178	75	Ambühl, 1958
Clear	14.9.52	14.1	9.0	16.0	153	35	ILSS, unpublished
Palette	22.8.28	13.8	9.0	13.4	146	34	Juday & Birge, 1932
Clear	15.7.29	13.8	8.0	15.2	147	38	Scott, 1931
Millstätter See	22.8.63	13.8	9.0	15.2	153	36	Findenegg, unpublished
Cook	20.7.53	13.7	6.0				Eberly, unpublished
Zürichsee	26.6.30	13.7	5.				Minder, 1934
O-numa	1.8.33	13.6	3.0	18.8	160	81	Yoshimura, 1938
Elkhart	23.8.09	13.6	10.0	12.4	136	31	Birge & Juday, 1911
Zürichsee	July.23	13.6	10.				Minder, 1926
Pipurger See	13.10.31	13.6	9.0	8.6	135	30	Leutelt-Kipke, 1934
Pipurger See	19.6.32	13.6	5.0	11.4	145	53	Leutelt-Kipke, 1934
Sumiyoshi-ike	7.8.29	13.5	2.4	24.4	165	85	Yoshimura, 1938
Garvin	27.6.06	13.5	4.5	15.0	143	54	Birge & Juday, 1911
Sempachersee	10.6.58	13.5	5.0	16.0	151	50	Ambühl, 1958
Tsuta-numa	31.7.35	13.4	3.0	13.1	140	71	Yoshimura, 1938
Elkhart	2.9.08	13.4	10.0	11.7	128	29	Birge & Juday, 1911
Gordy	26.7.52	13.3	4.0	19.0	153	65	ILSS, unpublished
Silver	27.8.08	13.2	8.0	13.3	139	34	Birge & Juday, 1911
Silver	28.8.31	13.2	9.0	14.7	143	31	Juday & Birge, 1932
Millstätter See	17.9.32	13.2	10.	16.	149	30	Findenegg, 1934
Pleasant	4.8.51	13.1	6.0	22.0	160	46	ILSS, unpublished
Black Oak	14.8.07	13.0	9.0	10.2	128	31	Birge & Juday, 1911
Hancza	18.8.31	13.0	15.	6.7			Kozminski, 1932
Klopeiner See	21.8.63	12.8	9.0	15.7	142	39	Findenegg, unpublished
Faaker See	19.8.63	12.8	8.0	17.5	147	47	Findenegg, unpublished
Crooked	13.7.51	12.8	8.0	14.4	134	36	ILSS, unpublished
Klopeiner See	22.8.31	12.7	10.	15.	139	33	Findenegg, unpublished

to have little in common except their similar basin shape. They have different origins and a wide range of location, altitude, and chemical conditions.

A general summary is presented in Table 3. Observed oxygen maxima range from the 12.7 to 36.5 mg/L with a mean of 17.2 and a median of 15.7. The highest oxygen concentrations have been found in the Indiana

TABLE 3. Summary of average conditions. A = area; z_m = maximum depth; z_r = relative depth; n = number of lakes.

Region	n	O ₂ mg/L	Max. O ₂ mg/L	A ha	z_m m	z_r %
Indiana	12	18.0	33.2	54	16.3	2.81
Wisconsin	13	17.8	36.5	83	20.5	3.22
Alps	15	16.9	29.4	910	51.6	3.14
Japan	12	15.8	22.4	38	30.7	7.70
USSR	1	15.5	16.8	3	23.	11.76
Poland	1	13.0	13.0	305	108.	5.51
mean		17.2		299	32.1	4.30
median		15.7		20	21.6	3.31

and Wisconsin lakes, but it is probably true that the oxygen patterns of these lakes have been studied more extensively than some of the others. Higher values than those now known could easily occur in some of the Alpine and Japanese lakes as well as in the small woodland lakes in Russia.

The lakes range in size from less than 3 ha to over 6000 ha, with a median size of 20.2 ha. The majority (29 or 56%) are under 30 ha. The decrease in the number of lakes of larger size is quite obvious in the US and Japanese series (see Table 4). The presence of the 5 large Alpine lakes is enigmatic because the highest oxygen concentrations of the Alpine group were observed in these large lakes. In depth the lakes ranged from 6 m to over 140 m with a mean value of 32 m and a median of 22 m. The Alpine lakes also have the greatest average depth (the one Polish lake is not so deep as several of the Alpine lakes).

Depth-area relationships are important in comparing the morphometry of different lakes. The area of the lakes in this study is plotted against maximum depth in Figure 3. A line showing the depth-area relationship of the Japanese lakes is given, because these lakes are so distinctly different from the others. Mean depth which relates volume with area is quite useful, but unfortunately this parameter was not

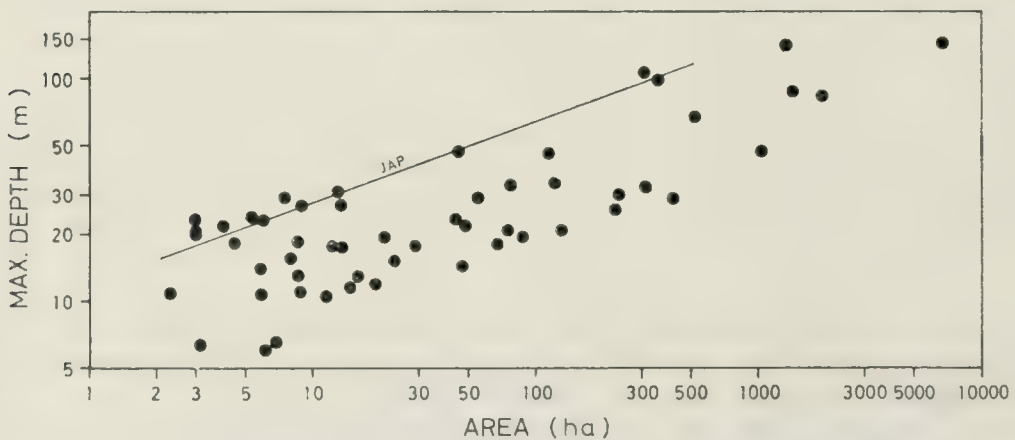


FIG. 3. Area of lakes with metalimnetic oxygen maxima plotted against maximum depth.

available for all of the lakes. Volume development ($3\bar{z}/z_m$) gives an indication of basin shape, which is rather reliable for smaller lakes. For small lakes with a volume development greater than unity, the maximum depth alone in relation to the area is a comparable index. For the lakes for which mean depth is available, 36 (90%) have volume developments greater than 1.00.

In earlier papers the ratio $z_m/\sqrt{\text{area}}$ was used. The concept of *relative* depth developed by Hutchinson (1957) is more meaningful and may be used instead. Relative depth (z_r) is determined from the relationship

$$z_r = 50z_m\sqrt{\pi}(\sqrt{A})^{-1}$$

in which the maximum depth is expressed as a percentage of the mean diameter. The relative depth ranged from 1.28 to 11.76 with a mean value of 4.30 and a median of 3.31. The highest indices are found in the Japanese lakes and in the Russian lake. In small lakes the type of stability conducive to optimal accumulation of oxygen in the metalimnion can develop only in lakes with rather high depth-area proportions. In larger lakes relative depth is less important, because the greater depth that is usually associated with large lakes is adequate for a stable stratification.

Except for the single examples from Poland and Russia, the lakes of this survey are located in three well-defined geographical and topographical regions—north-central glaciated United States, central European Alps, and Japanese mountain lakes. The Indiana and Wisconsin lakes are so similar that they are treated as a single group (referred to simply as US lakes) in the comparative studies that follow. The US lakes have a common origin (glacial ice-block) and occur within an area comparable to that represented by the Alpine or Japanese lakes. The US lakes are also subject to roughly the same climatic conditions and are similarly influenced by the hydrological and chemical conditions of the glacial drift in which they are located. Hancza and Belowod-See are not included, but from the data given in the tables one can readily see how they compare with the three main groups.

MORPHOMETRY AND OXYGEN MAXIMA

From an inspection of the distribution of lakes by area, four size groupings were established to present the data in Table 4. In the US and Japanese lakes, the highest oxygen concentrations were observed in the small lakes, with a general decrease in oxygen with an increase in size of the lake. No such relationship seems to exist in the Alpine lakes, where the highest values observed occurred in the large lakes. A small surface area minimizes the effect of the wind in producing turbulence that would disrupt oxygen stratification. The fact that there is no clear relationship between area and high oxygen values suggests that some other factor could be restricting the effect of the wind on the Alpine lakes. In lowland lakes the presence of trees and hills that shield the lake from the more direct action of the wind is very important, especially in small lakes. Apparently the protection afforded by the mountain environs is quite significant in producing somewhat uniform conditions as far as wind-

induced turbulence is concerned, independently of the size of the lakes. In this respect the difference between small and large mountain lakes must be much less than the corresponding difference between small and large lowland (or level land) lakes.

The depth of the oxygen maximum generally increases with the increase in area of the lake, though this is less clear in the Alpine lakes than in the others. There is, however, some variation, especially in the US small lakes where the standard deviation of the mean is 1.6 m and

TABLE 4. Average conditions in lakes by region and surface area classes.

Area <i>ha</i>	Number				Maximum depth (m)			
	US	ALP	JAP	total	US	ALP	JAP	mean
0-30	15	4	10	29	13.1	17.9	22.2	16.9
30-150	7	4	1	12	25.6	25.9	47.0	27.5
150-750	3	2	1	6	29.1	48.0	99.0	47.1
over 750		5		5		100.4		100.4
total:	25	15	12	52				
mean:					18.5	51.5	30.7	32.1
median:					17.9	30.0	23.6	21.6
	Depth O ₂ maximum (m)				Relative depth (%)			
	US	ALP	JAP		US	ALP	JAP	
0-30	5.2	5.1	3.9		3.52	5.55	8.02	
30-150	8.0	6.6	5.0		2.60	2.66	6.20	
150-750	8.5	6.0	12.0		1.47	2.13	4.68	
over 750						1.98		
				mean:	3.02	3.14	7.70	
				standard deviation:	1.11	2.34	1.69	
				coefficient of variation (%):	37	75	22	
				median:	2.94	2.55	7.90	
	Oxygen (mg/L)				Maximum O ₂ (mg/L)			
	US	ALP	JAP	mean	US	ALP	JAP	
0-30	19.3	16.0	16.1	18.4	36.5	19.7	22.4	
30-150	14.4	16.8	14.3	15.3	18.0	20.0	14.3	
150-750	13.9	13.7	14.4	13.9	16.0	14.6	14.4	
over 750		17.6		17.6		29.4		
mean:	17.9	16.9	15.8	17.2				
	Saturation (%)				Absolute saturation (%)			
	US	ALP	JAP	mean	US	ALP	JAP	mean
0-30	209	143	178	198	78	48	83	78
30-150	150	177	160	159	40	61	61	47
150-750	143	156	135	145	36	56	28	40
over 750		199				47		
mean:	191	183	173	186	67	51	77	64

the coefficient of variation (V) is 31%. The depth of the oxygen maximum depends on the depth of the thermocline, which in turn reflects the combined interaction of wind intensity, especially following spring circulation, and area of the lake. In the Alpine lakes, because of the reduced effect of the wind, depth of the metalimnion is more uniform and without a significant relation to area.

The correlation of oxygen saturation with area follows the same general pattern as oxygen concentrations. The higher oxygen value of the largest Japanese lake represents a lower saturation level than that in the next smaller lake because of the greater depth and colder temperature. For the same reason the very high oxygen concentrations in the large Alpine lakes, which average 199% saturation, represent only 47% absolute saturation, the lowest value in the Alpine series. The average absolute saturation in the Japanese lakes is the highest of the entire group because of the reduced depth of the oxygen maxima.

The relation of area to depth, both maximum and relative, shows the expected increase in maximum depth and decrease in relative depth with increase in area. If the depth-area ratio were constant, one would expect to find the same relative depth in all lakes. The difference in this ratio that is actually found suggests that the small lakes are unusually deep for their size and that, while large lakes usually have a very small relative depth (e.g., see Hutchinson, 1957: Tables 1 and 2), the larger lakes in this study that have oxygen maxima have relative depths greater than usual for lakes of that size. Actually, the distinctiveness of the morphometry of the large lakes possessing oxygen maxima may be greater than that of the small lakes. In the more productive glacial region of the US, small lakes would tend to fill in and disappear rather quickly, so that only those deeper and more oligotrophic small lakes would still be in existence at the present time.

In order to test this idea, the relative depths of the 25 US lakes with oxygen maxima were compared with the same parameter of 250 lakes without oxygen maxima from the same area. Data for the 78 Indiana lakes were taken from Frey (1955a), for 84 southeastern Wisconsin lakes from Juday (1914: Tables 1 and 2), and for the 88 northeastern Wisconsin lakes from Juday (1914: Table 3) and Juday and Birge (1941). The mean relative depths of these lakes by area and the statistical treatment is given in Table 5. P is the probability that the two samples (with and without oxygen maxima) could have been selected randomly with mean relative depths differing as much as or more than the difference actually obtained. A low P value is taken as indicating that relative depth is a significant factor in the development of a metalimnetic oxygen maximum. The 250 lakes represent lakes that have had some interest to limnologists, hence their inclusion in the sources cited above. Though no attempt was made to assess the extent to which they are representative of all the lakes of Indiana and Wisconsin, it was assumed that the 250 lakes are a reliable random sample, since the original lists were compiled neither on the basis of relative depths nor on the nature of the oxygen profile.

The difference between the mean relative depth of the 25 lakes with oxygen maxima and that of the 250 lakes without a known maximum is quite significant ($P = <.001$). But if one compares the various size

TABLE 5. Comparison of the relative depths of 25 lakes having metalimnetic oxygen maxima with 250 lakes without a known oxygen maximum. n = number of lakes; \bar{z}_r = mean relative depth; S.D. = standard deviation; V = coefficient of variation ($\times 10^2 = \%$); P = probability that differences are from chance alone.

Area <i>ha</i>	Indiana					S. E. Wisconsin					N. E. Wisconsin					US Lakes—Total				
	n	\bar{z}_r	S.D.	V	P	n	\bar{z}_r	S.D.	V	P	n	\bar{z}_r	S.D.	V	P	n	\bar{z}_r	S.D.	V	P
0-30																				
without max.	22	3.23	1.54	.49		15	2.97	1.34	.45		21	4.46	3.50	.79		58	3.61	2.49	.69	
with max.	9	3.01	0.77	.26	.7-.6	5	4.40	0.86	.20	.2-.1	1	3.77				15	3.52	1.02	.29	.9-.8
30-150																				
without max.	45	1.99	0.77	.38		48	1.51	0.70	.46		28	1.08	0.71	.66		121	1.59	0.81	.51	
with max.	2	2.49				3	3.14				2	1.92				7	2.60	0.71	.27	<.01
150-750																				
without max.	11	1.17	0.38	.32		21	0.77	0.39	.51		39	0.64	0.31	.48		71	0.76	0.39	.51	
with max.	1	1.62									2	1.40				3	1.47			<.01
Total																				
without max.	78	2.22	1.23	.55		84	1.59	1.07	.67		88	1.69	2.36	1.40		250	1.82	1.70	.93	
with max.	12	2.81	0.84	.30	<.001	8	3.93	0.91	.23	<.001	5	2.08	0.88	.42	.8-.7	25	3.02	1.11	.37	<.001

categories within the two groups of lakes, different results appear. The number of lakes of each size group with oxygen maxima suggests the frequency of occurrence of oxygen maxima in lakes of that size. In lakes under 30 ha, 15 of a total of 73 lakes are known to have developed oxygen maxima (21% or 1:4.9). The corresponding frequency in lakes of 30-150 ha is 5.5% (1:18.3), and for lakes of 150-750 ha, 4.1% (1:24.7).

The mean relative depth of both groups of lakes less than 30 ha is very close, in fact, that of the lakes without oxygen maxima is even greater. This seems to support the contention that small lakes within the areas studied generally have a high relative depth. With increasing area, *P* values become significant, indicating that larger lakes with oxygen maxima have significantly different morphometry than lakes of similar size without maxima.

The situation in the lakes of Indiana and southeastern Wisconsin parallels that of the total for the whole group. The difference between the 5 small, southeastern Wisconsin lakes and the others of that size group is influenced by the fact that 4 of the lakes with oxygen maxima belong to the rather compact Waupaca chain with uniformly high relative depths. In northeastern Wisconsin the average relative depth of the 21 small lakes without oxygen maxima is considerably greater than that of the single lake in this size class with an oxygen maximum. The relative depth of these small lakes is also greater than that of similar sized lakes in the other two areas, while the relative depth of the larger size categories is lower than similar lakes in Indiana and southeastern Wisconsin.

Geologically Indiana and southeastern Wisconsin are older than northeastern Wisconsin (i.e., they have been exposed earlier by the northward retreat of the glacier). The terrain is more level and a greater degree of eutrophy exists in the lakes. This is reflected in the absence of very shallow small lakes and the reduced depth of the deeper small lakes in the area. These two regions are also more suitable for agriculture and settlement, which would also seem to have the same effect on small lakes. Agriculturally induced erosion and fertilizers entering the lakes would contribute toward eutrophication and more rapid filling. Soil drainage for agricultural purposes has eliminated many very shallow lakes.

Northeastern Wisconsin is heavily forested and supports less agriculture. Nutrient levels are low (e.g., average calcium is about 1/10 that of lakes in southeastern Wisconsin). Consequently, there is less alteration of the original morphology due to filling by both allochthonous and authochthonous sediments. The very small lakes are converted to bogs of various types. The small lakes that remain are deep with maximum depths probably very close to the original. The average is weighted very heavily by the presence in the sample of Lake Mary (1.2 ha, 21.5 m) and Rose Lake (1.43 ha, 15.7 m). Morphometrically the small deep lakes in northeastern Wisconsin comprise a rather unique group of lakes. One is tempted to predict that further study would disclose more cases of metalimnetic oxygen maxima in this group.

As a group, the 88 northeastern Wisconsin lakes without oxygen maxima are more variable ($V = 140\%$) than lakes from the other two areas. This trend is reflected also in the lakes with oxygen maxima, with the 8 lakes from southeastern Wisconsin being the most uniform ($V = 23\%$).

Throughout the sampling the lakes with oxygen maxima show much less variability than the other lakes. The difference between the variability of lakes with and without oxygen maxima generally decreases with increase in size.

The distribution of relative depth in the US, Alpine, and Japanese lakes, as well as the correlation of oxygen conditions with relative depth is shown in Table 6. The range and distribution of relative depth in the US and ALP lakes is very similar, as is also indicated by the mean values. The Japanese lakes exhibit a much greater relative depth (mean 7.70). Whether this differs significantly from the average of Japanese lakes in general was not determined. Considering relative depth only, the Japanese lakes are the most uniform group ($V = 22\%$). The much greater variability of relative depth among the Alpine lakes ($V = 75\%$) is taken as another indication of the less important role that morphometry plays in the development of the oxygen maximum in these lakes.

In the US and ALP lakes, oxygen maxima are most likely to be found in lakes where $z_r = 1.50 - 3.50$. The greatest oxygen maximum observed in the US was in a lake with a relative depth of 3.96, in the Alps in a lake with a z_r of 1.29, and in Japan in a lake with a z_r of 7.60. The average oxygen concentrations in the various relative depth categories show nearly the same optima. In the US lakes, an optimum at a relative depth of 4% is very clear. The slightly higher value at $z_r = 6$ represents only a single lake with a relative depth of 5.64 and is not sufficient to establish a definite trend in that category.

In Figure 4 every oxygen maximum is plotted against its corresponding relative depth along with the mean curves for each series of lakes. No clear optimum is indicated by the Japanese series, though a definite optimal size was shown earlier. In the Alpine lakes, highest average oxygen concentrations were found in lakes with very low and very high z_r values, with the lowest oxygen concentrations being found at the same relative depth that the highest maxima were found in the US lakes. Since there are only 3 Alpine lakes with a z_r greater than 3.5%, it is doubtful that the concave curve

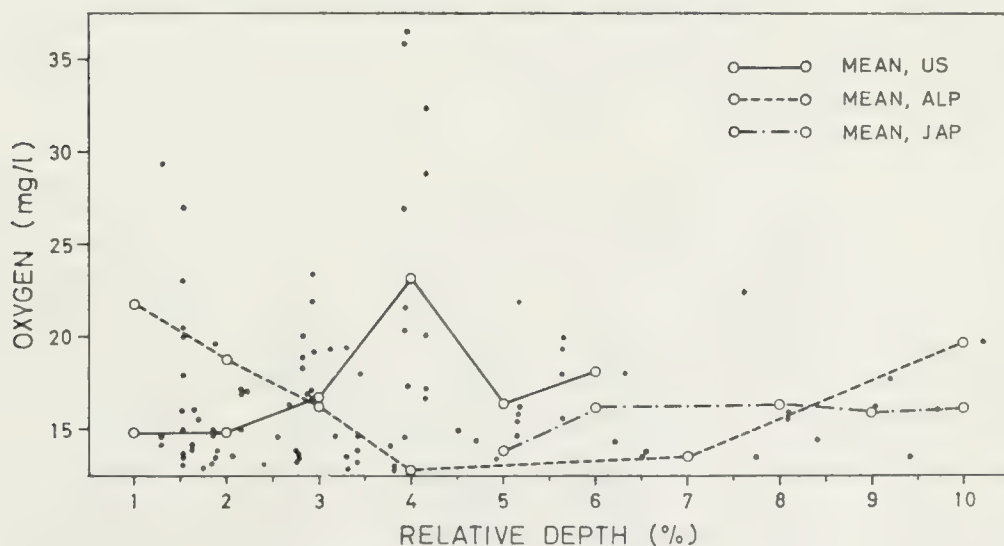


FIG. 4. Metalimnetic oxygen maxima and mean oxygen maxima by relative depth of lakes.

shown in the figure has much significance, but it appears rather certain that relative depth *per se* has little effect on the variation of oxygen concentrations found in the metalimnion.

In summary, the highest concentrations of oxygen are clearly to be found in those US lakes less than 30 ha in area and with a relative depth of about 4%. In the Japanese lakes, highest values are definitely related to small size but not to relative depth. There does not appear to be any reasonable correlation of any morphometric factor in the Alpine lakes with variations in magnitude of the oxygen maxima.

STABILITY AND OXYGEN ACCUMULATION

Area, to a large extent, determines the distance (fetch) over which the wind may act in producing surface turbulence. In general, the greater the area the more pronounced is the effect of the wind and consequently the deeper the thermocline. If the thermocline lies below the compensation level, no oxygen maximum will occur. When a portion of the phototrophic zone extends below the thermocline, oxygen production can occur within the metalimnion. If respiratory processes are not so great as gross photosynthesis, a net excess of oxygen will result. Under conditions of minimal turbulence this oxygen will accumulate, producing the metalimnetic oxygen maximum.

Maximum stability (and consequently minimum turbulence) occurs as the thermocline approaches the center of gravity (Ruttner, 1963). Under such conditions, especially when the layer of oxygen production is just below the center of gravity, conditions for the retention and accumulation of oxygen seem to be optimal. Table 7 shows the results of the calculation of the center of gravity (z_g) for 6 lakes, along with the highest oxygen maxima observed and other relevant data and calculations. The center of gravity is found by multiplying the percentage of the total volume within

TABLE 7. Stability and center of gravity, compared with other measurements, in 6 lakes with high oxygen maxima. S = stability of lake in meter-tons; S_r = stability relative to surface area in $\text{g}\cdot\text{cm}/\text{cm}^2$; $S_{r'}$ = stability relative to volume in $10^5 \text{ g}\cdot\text{cm}^3$; z_g = depth of center of gravity of water mass; $z_{g'}$ = geometric center of gravity; z_{max} = depth of oxygen maximum; z_t = estimated depth of thermocline; z_r = relative depth in percent.

	McLish	Beasley	Myers	Marl	Knights	Otter
S	7902	2681	9781	2315	1191	486
S_r	576	464	339	272	140	84
$S_{r'}$	5.65	5.21	4.93	5.06	3.01	2.24
z_g	5.9	4.4	5.6	4.6	3.3	2.3
$z_{g'}$	6.2	4.5	5.8	5.0	3.5	2.4
$10^2 \cdot (z_g - z_{g'}) / z_m$	1.7	0.7	1.1	2.2	1.5	0.9
O_2	32.4	21.9	23.3	20.0	36.5	27.0
z_{max}	6.0	5.0	8.0	4.0	4.5	4.0
z_t	5.2	5.3	5.5	4.7	4.1	4.4
$z_g - z_t$	+0.7	-0.9	+0.1	-0.1	-0.8	-2.1
$z_g - z_{\text{max}}$	-0.1	-0.6	-2.4	+0.6	-1.2	-1.7
$z_t - z_{\text{max}}$	-0.8	+0.3	-2.5	+0.7	-0.4	-0.4
z_r	4.16	5.16	2.94	5.64	3.96	3.94

each stratum by the absolute density of water at the mean temperature of the stratum, adding the results cumulatively from the surface downward, determining the percent of each cumulative sum, and plotting a hypsographic curve showing the relative percent by weight of the water mass above each depth. This is very close to the 50% level determined from a volume-based hypsographic curve. The "geometric" center of gravity (z_g), determined according to Eckel (1950), may differ somewhat from the actual center of gravity of the water mass. An indication of the stability of the lake is afforded by the degree of coincidence of the two centers of gravity. In the table the difference in depth between the two centers of gravity is expressed as a percent of the maximum depth ($10^2 \cdot (z_g - z_{g'})/z_m$). The two points are very close in all the lakes.

In Myers and McLish lakes the thermocline lies just above the center of gravity (z_g), while in the others the thermocline is below by as much as 2.1 m in Otter Lake (19.6% of maximum depth). In all but Marl Lake the oxygen maximum is below the center of gravity, and in Marl and Beasley the oxygen maximum is above the thermocline. The absolute stability S as ton-meters ($10^8 \text{ g} \cdot \text{cm}$) was calculated from the Schmidt equations according to the method of Eckel (1950). Relative stability is expressed in terms of the surface area (S_r) as $\text{g} \cdot \text{cm}/\text{cm}^2$ and in terms of the volume of the lake (S_v) as $\text{g} \cdot \text{cm}/\text{m}^3$. Relative stability, which may be regarded as a measure of the intensity of stratification, is a useful means of comparing lakes irrespective of size.

In all three ways of stating stability, the highest values are obtained for McLish Lake. Otter Lake, which ranks lowest in all measures of stability, has produced some very high oxygen maxima in the past. This is likely due in part to the fact that Otter Lake is long and narrow and is oriented in a general north-south direction so that little more than 100 m of surface is exposed to the prevailing westerly winds. Furthermore, dense tree cover exists on the shore, resulting in practically no wind disturbance at all.

Another direct measurement of the amount of turbulence present in the lower metalimnion is through the McEwen-Hutchinson determination of the clinolimnetic coefficient of eddy conductivity (Hutchinson, 1941, 1957). After subtracting the molecular thermal conductivity of water (0.12×10^{-2}), the mean values of the coefficient for Myers Lake during the summers of 1952-1955 were 0.17, 0.09, 0.50, and $0.24 \text{ g} \cdot \text{cm}/\text{sec} \times 10^{-2}$ (Eberly, 1959). The coefficient had a value of 0.05 for the clinolimnion of McLish Lake (6-10 m) during the summer of 1961. Though the values for each stratum may not be too meaningful, the lowest values in every case existed near the level of the oxygen maximum. One is tempted to suggest that turbulence mechanisms of some sort aid in concentrating the plankton organisms at the plane of least turbulence. When ecological conditions within this "eddy trap" are optimal for the plankton species present, massive blooms can develop. That the highest concentrations of oxygen usually occur just above the greatest mass of phytoplankton is perhaps due to a self-shading effect within the bloom itself.

It appears that optimal conditions for the retention and accumulation of oxygen occur when the thermocline lies at or just above the center of gravity and the level of maximum photosynthesis is below this within 2

or 3 m. However, the presence of an ideal morphometry *per se* will not produce an oxygen maximum. The ecological factors most significant in the production of oxygen in the metalimnion are light intensity, temperature, and the nutrient composition of the water.

CLASSIFICATION OF METALIMNETIC OXYGEN MAXIMUM TYPES

Chiefly from a study of some of the Indiana and Wisconsin lakes, four distinct types of metalimnetic oxygen maxima seem to exist. They differ not only in the time of the year they appear, but in depth, temperature, and light conditions associated with the production of the oxygen. Very high oxygen values can occur in each type. At least three of the types are represented in the lakes in which the oxygen concentrations exceeded absolute saturation.

I. *Pseudo-metalimnetic oxygen maximum.* In small, well protected lakes, secondary thermoclines occasionally develop very near the surface, thus placing the lower portion of the epilimnion under the same degree of protection and stability as the normal metalimnion. Such conditions are usually temporary, since wind-induced circulation eventually incorporates this "pseudo-metalimnion" back into the epilimnion. Oxygen maxima that develop under these conditions usually reach their climax during June or July and disappear by August. The phytoplankton is similar to the usual summer epilimnetic plankton. Light attenuation is often quite extreme because of the dense plankton bloom that develops within these very stable layers. In Wyland Lake, for example, the 1% level was at 2.9 m during the height of the oxygen maximum cycle during 1955. Oxygen maxima do not develop regularly every year. Oxygen concentrations can reach fairly high levels rather quickly following a period of intense calm warm weather during which a secondary thermocline often forms. Strata of high oxygen concentration are usually very thin. Oxygen data for Wyland and Taylor lakes (Table 8) illustrate this type of oxygen maximum. This is probably a common type in small, shallow lakes.

II. *Temporary sub-climax oxygen maximum.* Under the protection imposed by thermal stratification, part of the normal spring plankton com-

TABLE 8. Pseudo-metalimnetic oxygen maxima in Wyland and Taylor lakes. Oxygen values in mg/L; vertical lines indicate extent of metalimnion; z_1 percent = depth of 1% surface illumination.

Depth <i>m</i>	Wyland 1955					Taylor 1960	
	23.6	28.6	11.7	20.7	25.7	8.7	8.8
0	13.6	14.9	11.2	10.5	10.0	8.7	10.8
1	13.1	16.0	11.5	10.2	10.1	8.6	11.5
2	18.7	18.5	19.3	12.4	10.3	8.7	11.3
3	14.5	16.0	6.9	13.3	9.3	17.0	6.7
4	12.4	6.2	1.2	2.3	0.4	1.8	0.6
5	0.9	0.6	0.4	0.5	0.1	0.2	0.1
6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
z_1 percent			2.9	4.2		5.2	4.6

munity in very transparent lakes may persist in the metalimnion during part of the summer. With increased temperature and light penetration, production of oxygen may reach a maximum in June or July. Even though adequate light still penetrates the metalimnion and there is no evidence of increasing turbulence (the level of oxygen production is located well below the thermocline), the maximum gradually disappears, accompanied by a decline in the plankton community. There is no development of a distinctive, permanent summer metalimnetic phytoplankton community. Perhaps the plankton community fails to maintain itself because of the gradual depletion of the nutrient supply. Because of the high transparency, the oxygen maximum is fairly thick, with rather uniform oxygen concentrations throughout. This type of maximum can occur in relatively deep lakes with low nutrient levels.

A good example of the sub-climax oxygen maximum is Still Lake (Table 9). The highest oxygen concentration was observed on 2 June, the earliest date the lake was sampled. On that date 4% of the surface illumination was still present at the depth of the maximum at 7 m. The average depth of 1% illumination during the entire summer of 1961 was 11.5 m. The larger lakes of the Waupaca (Wisconsin) chain, Long and Rainbow, have oxygen maxima resembling this type (Table 10). Highest oxygen values are usually reached by early July. In 1959 the highest concentration observed in Long was 10.9 mg/L, in Rainbow 11.5 mg/L. Whether greater maxima had developed earlier in the summer is not known. Under the influence of secondary thermoclines, both lakes developed smaller oxygen maxima above the normal metalimnetic maxima. The 1% light level was 9.1 m in Long and 9.8 m in Rainbow.

TABLE 9. Temporary sub-climax oxygen maximum in Still Lake, 1961. Oxygen values in mg/L; vertical lines indicate extent of metalimnion; z_1 percent = depth of 1% of surface illumination.

Depth <i>m</i>	June			July		Aug.
	2	16	30	14	28	21
0	9.5	8.7	8.3	8.3	8.5	8.4
1	9.6	8.8	8.5	8.3	8.6	8.4
2	9.6	8.6	8.5	8.3	8.8	8.4
3	9.9	8.6	8.7	8.1	8.7	8.4
4	10.8	8.9	8.4	7.8	8.5	8.4
5	12.3	12.3	8.5	7.9	9.9	8.4
6	14.6	14.0	12.1	9.7	10.3	7.7
7	14.8	14.7	12.5	11.8	11.0	6.1
8	13.8	13.7	13.4	11.8	9.6	5.5
9	13.1	13.1	13.2	12.4	11.1	5.5
10	12.6	11.6	12.5	12.1	10.3	6.0
11	12.1	11.5	11.2	11.3	10.2	
12	11.3	10.2	7.9	9.6	8.7	1.0
13				2.7		
14	6.1	7.1	1.1	1.8	1.0	0.3
15						
16	3.1	0.5	0.2	0.1	0.0	0.0
z_1 percent	11.0	10.7	12.5	13.2	10.3	9.4

TABLE 10. Dissolved oxygen concentrations observed in some Waupaca lakes in 1959. Oxygen values in mg/L; vertical lines indicate extent of metalimnion; z_1 percent = depth of 1% of surface illumination.

Depth <i>m</i>	Beasley	Knights	Marl	Otter	Long	Rainbow
	July 27	July 28	Aug. 6	Aug. 2	July 30	July 21
0	8.6	9.7	9.3	9.9	8.9	9.0
1	8.4	9.8		10.0		8.8
2	8.9	10.0	9.5	10.1	10.6	8.9
3	9.4	12.5	8.4	12.1	10.9	9.0
4	12.7	17.4	10.7	14.5	10.0	10.5
5	15.3	17.1	19.4	7.5	10.1	11.3
6	8.3	9.8	18.1	3.4	10.4	10.7
7	5.1	5.4	16.7	1.5	7.4	11.5
8	0.6	3.8	15.2		0.8	11.2
9	0.4	1.1	10.4		0.2	8.7
10	0.4	0.4			0.2	4.5
11	0.2	0.3				3.0
12			0.4		0.1	0.7
13						
14						
15						0.4
16					0.3	
17						
18						0.0
19						
20					0.5	
21						0.0
z_1 percent	9.85	7.5	8.95	9.0*	9.1	9.8

* Estimated

III. *Permanent climax oxygen maximum.* In this type the oxygen maximum is present throughout most of the period of summer stratification, reaching the greatest values in August or September. The maximum persists until the beginning of fall circulation. Nutrient conditions are suitable for the maintenance of a permanent metalimnetic phytoplankton community, which is often dominated by distinctive forms that are subordinate at other depths or times of the year. The species composition of a plankton community is determined largely by the chemical composition of the water (i.e., the nutrient supply available). Two types of communities occur in most of the glacial lakes of the US, one dominated by diatoms and the other by blue-green algae. Both types are represented in the lakes with metalimnetic oxygen maxima. Very high oxygen concentrations have been observed in both types. Because different temperature and light conditions prevail, the maxima produced by the two types of communities may be designated as subtypes of the permanent climax oxygen maximum.

IIIa. *Diatom maximum.* The diatom communities producing this type of oxygen maximum are similar to the communities of the sub-climax type (Type II), but they are stable and permanent throughout the summer. The best known examples of this type in the US lakes are the four smaller

TABLE 11. Dominant metalimnetic net phytoplankters in Waupaca lakes, as 10⁴ individuals per liter.

	Depth (m)						
	3	4	5	6	7	8	9
Beasley							
<i>Fragilaria</i>	5.6	11.6	11.6	25.0	17.0	7.9	
<i>Asterionella</i>		0.2	6.5	9.8	8.5	3.2	
<i>Dinobryon</i>	0.7	5.8	3.0	5.3	3.3	1.7	
<i>Ceratium</i>	0.5	0.7	0.3	0.2	0.1	0.1	
Knights							
<i>Fragilaria</i>	10.9	2.7	5.4	6.4	38.7	17.8	8.7
<i>Dinobryon</i>	2.4	7.8	2.7	5.4	3.7	2.0	1.7
<i>Ceratium</i>	1.2	0.2	0.4	0.2	0.3	0.1	
<i>Chrysosphaerella</i>	1.1		0.3	0.2	0.3	0.1	
<i>Asterionella</i>		0.2					
Marl							
<i>Fragilaria</i>	0.2	0.5	1.4	1.3	1.4	0.4	0.4
<i>Dinobryon</i>			0.1	2.0	5.1	6.7	3.3
<i>Glenodinium</i>					0.1	0.2	
Otter							
<i>Fragilaria</i>	8.9	7.7	4.1	5.0	3.1		
<i>Dinobryon</i>	0.5						
Long							
<i>Fragilaria</i>		2.9	3.6	3.9	1.9	2.2	3.2
<i>Dinobryon</i>		4.2	4.3	1.5	1.0	1.9	0.4
<i>Asterionella</i>		0.2	1.9	5.8	7.3	5.3	3.3
<i>Ceratium</i>		0.2	0.3	0.3	0.1	0.1	
Rainbow							
<i>Fragilaria</i>		0.4		0.5	0.2	0.6	0.8
<i>Dinobryon</i>					0.7	0.8	0.2
<i>Ceratium</i>				0.1	0.1		

lakes of the Waupaca chain—Knights, Otter, Beasley, and Marl. Besides the extensive data by Birge and Juday (1911) on these lakes, there are those obtained by the writer in 1959 (Table 10). The oxygen maxima occur at a depth of 3.5 to 5.0 m, generally within a temperature range of 15-20°C and light intensities of 9-28% (1959 measurements only). At the lowest depth that the oxygen concentration exceeded 100% saturation the mean light intensity was $6.2 \pm 2.7\%$. Oxygen production is reduced or inhibited at depths where light intensity falls below about 5%, while the depth of maximum production seems to be determined more by a temperature optimum than by light. At the depth of the temperature optimum, however, production is generally proportional to the light intensity. The net plankton is clearly dominated in all lakes by *Fragilaria*, with significant numbers of *Asterionella* in Beasley (Table 11). The oxygen production potential of *Dinobryon* and *Ceratium* is not understood very well, though these forms were very numerous in the Waupaca lakes. An unusual form, *Chrysosphaerella longispina*, was abundant in Knights. *Anabaena* and other blue-greens were present only in small numbers. These observa-

tions on the phytoplankton agree favorably with the brief remarks of Birge and Juday (1911) and Smith (1920) on the plankton of these lakes. There does not appear to have been any significant change in community structure since the time of these early observations.

IIIb. *Oscillatoria maximum*. This type of maximum is produced by stenothermal blue-green algae communities dominated by *Oscillatoria agardhii* in US lakes and *O. rubescens* in the Alpine lakes. Myers and McLish lakes have been investigated quite extensively in respect to the development of the oxygen maximum. Much of the relevant data on these lakes has been published elsewhere (Eberly, 1959, 1963, 1964). Generally the oxygen maximum occurs at temperatures of 10-12°C and light intensities of 1-5% of surface illumination. In Myers Lake during the summer of 1955 the mean temperature at the depth of the maximum was $10.6 \pm 2.0^\circ \text{C}$ with a mean light intensity of $1.5 \pm 0.8\%$. The corresponding mean values for McLish during the summer of 1961 were $11.7 \pm 1.5^\circ \text{C}$ and $2.0 \pm 1.0\%$. Our present knowledge of the ecological aspects of oxygen production in the metalimnion of these lakes is summarized in the next section.

PRIMARY PRODUCTION IN THE METALIMNION OF *Oscillatoria* LAKES

Primary productivity measurements have been carried out in Myers and McLish lakes using both light-dark bottle oxygen measurements and C^{14} -labeled bicarbonate (Table 12). In order to compare results of the two procedures, a satisfactory photosynthetic quotient (PQ) must be established. Table 13 shows the results of the reciprocal conversion of direct oxygen measurements to equivalent carbon values and vice versa using various PQ ratios. Oxygen values represent gross oxygen production, while both total (light bottle only) and phototrophic (corrected for dark bottle uptake) carbon assimilation rates are presented. Excluding the early data for Myers Lake when the very productive deep-water *Oscillatoria*

TABLE 12. Mean daily gross production (late summer) in Myers and McLish lakes.

Depth <i>m</i>	$\mu\text{g O}_2/\text{L}$			$\mu\text{g C/L}$			
	Myers			McLish			
	1954	1955	1960	1960	1961	1961	1962
0	450	663	165	85	163	184	52
1				170	252	110	73
2	499		257	483	405	102	47
3			413	410	96	105	11
4	317	500	221	576	148	68	44
5	347	510	289	528	269	56	77
6	626	517	258	197	431	102	162
7		811	119		253	58	178
8	760	740	60		72	8	12
9	189	194					
10	142						
<i>g/m</i> ²	4.64	5.25	2.01	2.31	1.97	0.70	0.73

TABLE 13. Mean daily gross production as g/m². *Upper*—gross oxygen production in 3 Indiana lakes, and conversion of this to carbon at different photosynthetic quotients (PQ); *Lower*—C¹⁴ uptake in McLish Lake, and conversion of this to oxygen at various PQ's. Total = C¹⁴ uptake in light bottle only; Photic = light bottle uptake corrected for dark bottle uptake.

Lake and year	Gross oxygen production	Carbon equivalent at PQ		
		1.0	1.1	1.2
Myers, 1954	4.64	1.74	1.58	1.45
" 1955	5.25	1.97	1.79	1.64
" 1960	2.01	0.75	0.69	0.63
Taylor, 1960	2.12	0.80	0.72	0.66
McLish, 1960	2.31	0.87	0.79	0.72
" 1961	1.97	0.74	0.67	0.61
Mean of last 4 series	2.10	0.79	0.72	0.66

C ¹⁴ uptake		Oxygen equivalent at PQ					
Total	Photic	Total			Photic		
		1.0	1.1	1.2	1.0	1.1	1.2
25.8.61	—	0.70			1.87	2.05	2.18
24.7.62	0.98	0.79	2.62	2.87	3.05	2.11	2.32
30.7.62	0.89	0.66	2.38	2.61	2.77	1.76	1.93
Mean	0.94	0.72	2.50	2.74	2.91	1.91	2.10

bloom was present, the mean carbon equivalent calculated from oxygen data with a PQ of 1.1 is identical with the mean phototrophic uptake of C¹⁴. This seems to be a reasonable figure for plankton that is dominated by blue-green algae. Fogg (1953) cites a photosynthetic quotient of 1.08 determined for one species of Myxophyceae (*Synechococcus*). All subsequent conversion of oxygen data to carbon equivalents have been made using the PQ value of 1.1.

Assuming the correctness of the PQ value determined above, the agreement of the dark-corrected C¹⁴ rates with gross oxygen production during the later years is remarkable. Of course, simultaneous measurements with both methods would be the most reliable means to make the comparison, but it is safe to say even with the data at hand that C¹⁴ measurements in these lakes approximate the gross production rates much more closely than net production. Fogg (1963) has recently presented data which show the same results with laboratory cultures of *Anabaena cylindrica*. The degree to which radiocarbon measurements reflect actual photosynthesis rates depends on the amount of excretion by the algae in question of soluble metabolites containing labeled carbon. It may be that such excretion is very low in some filamentous Cyanophytes.

The oxygen maximum represents the total accumulation of net oxygen over a period of time. A determination of the rate of net production (P_N) based on 7 experiments in late summer during 1954-55 in Myers Lake

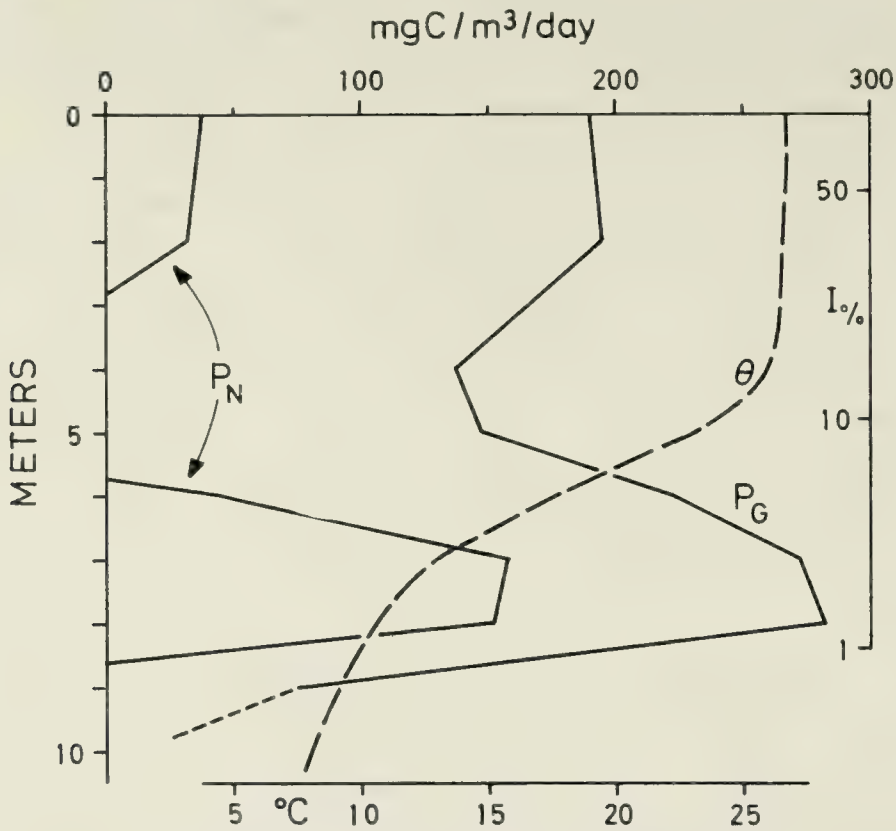


FIG. 5. Mean daily gross (P_G) and net (P_N) production in Myers Lake, late summer 1954-55.

disclosed the presence of 2 distinct strata with a net production of oxygen, one in the epilimnion immediately below the surface and the other in the lower part of the metalimnion (Fig. 5). Integration of these results with the volume of the lake led to the estimate that 73% of the total net production of oxygen occurred in the metalimnion (Eberly, 1959). The gross production curve (P_G) shows a decline in the lower epilimnion, which can no doubt be attributed to the diminution of light, since the phytoplankton of the epilimnion is usually rather uniform at all depths. A slight reduction in rate is often seen at the surface layer due to light saturation or photo-inhibition. The maximum rates of gross production in the metalimnion exceeded the maximum epilimnetic rates. Nearly half (46%) of the estimated gross production in the entire lake occurred in the metalimnion.

Comparable mean gross production curves for McLish Lake during 1960 and 1961 are shown in Figure 6. Though the depth of maximum metalimnetic production differed in the two years, the same general conditions of light and temperature prevailed. The average depth of the oxygen maximum during 1960 was more than a meter higher than in 1961. The curve obtained from C^{14} measurements (e.g., curve C_p in Figure 7) parallels the oxygen production curves very closely, except that the inhibition at the surface is not so evident in the three series thus far run on McLish Lake.

The photosynthetic efficiency at the depth of maximum oxygen production in the metalimnion can be approximated using average insolation

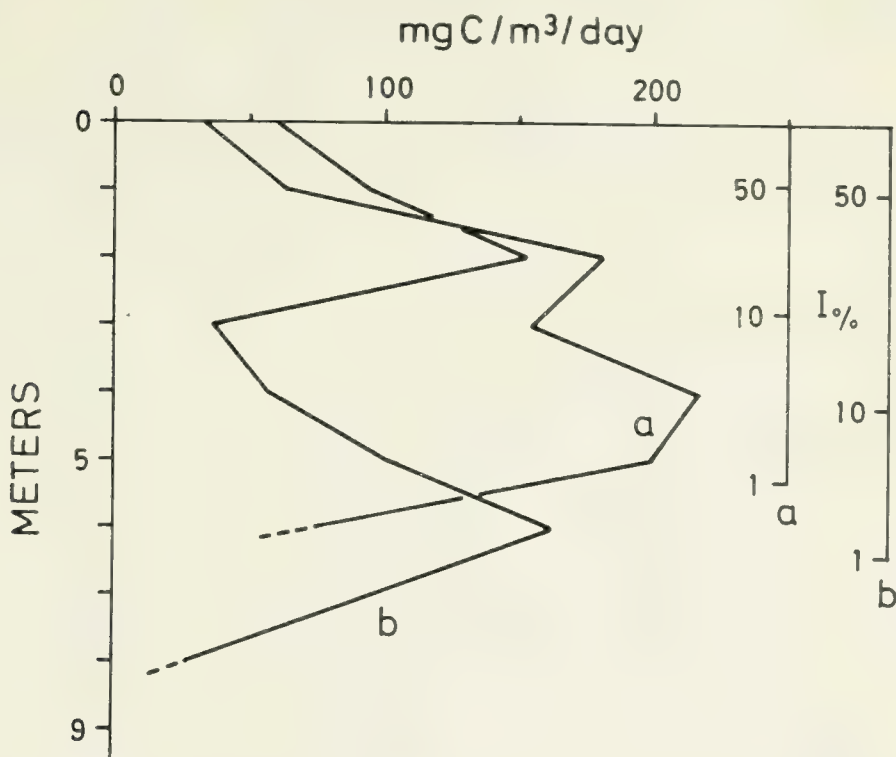


FIG. 6. Mean daily gross production (calculated from oxygen production data) and mean transparency (I_{percent}) in McLish Lake, late summer 1960 (a) and 1961 (b).

values given by Hutchinson (1957). Assuming a general loss by reflection of about 10%, the amount of absorbed radiation at the general latitude of McLish Lake during the latter part of July and August is about 5×10^6 cal/m²/day. The overall efficiency, with an average daily production of 0.7 g C/m², is about 0.13%. At a depth of 6 m where the maximum production occurred in 1961, average production amounted to about 130 mg C/m³ with about 3% of the absorbed radiation reaching this level during the experimental period. This represents a photosynthetic efficiency of 0.8%. In Myers Lake during the experiments of 1954-55 the maximum level of production was at 8 m with a mean production of about 280 mg C/m³. This represents roughly twice the efficiency of the 6 m stratum in McLish Lake, or about 1.7%. The total efficiency for Myers during this period with an average production of 1.7 g C/m², was about 0.32%. Though these figures are only approximations, they indicate the general order of magnitude represented in the deep metalimnetic strata. Nothing is so far known of the annual cycle of production in these lakes.

Since the phytoplankton of the metalimnion of McLish Lake (and Myers Lake during the period studied from 1951-1955) consisted almost wholly of *Oscillatoria agardhii*, any observations on metabolic activities in this region may be inferred to be reflections of the ecology and physiology of this one species. One of the problems concerns the presence of the great mass of algae at a depth about 1 m or so below the level of maximum oxygen production. Mention has already been made of the possible role of eddy currents in concentrating the plankton at particular levels. The *Oscillatoria* do not appear to be senescent. There is a very sharp decline in

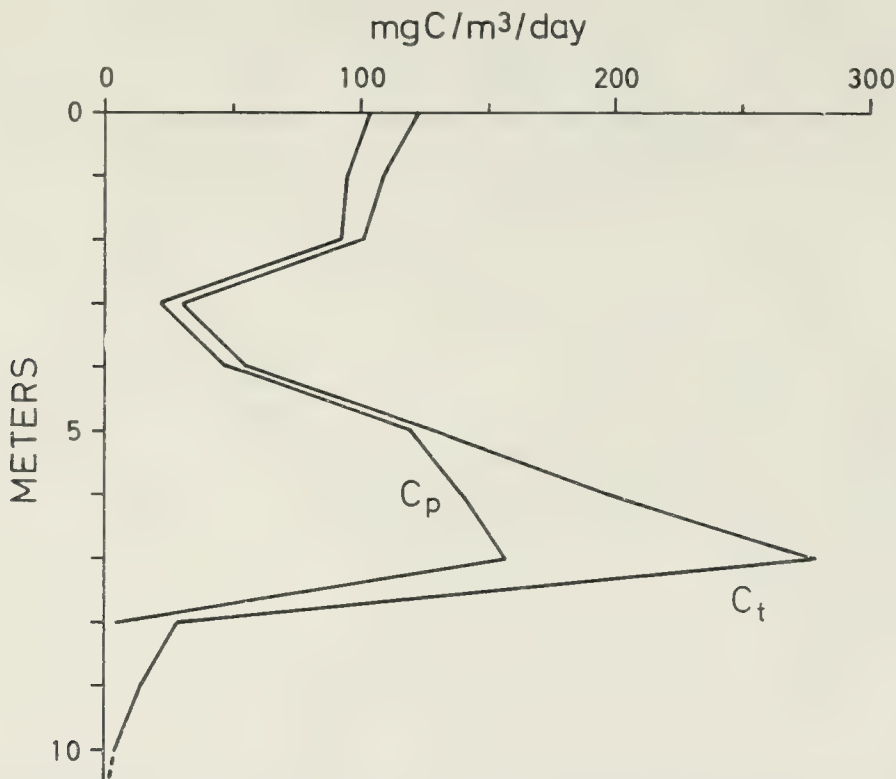


FIG. 7. Total (C_t) and phototrophic (C_p) carbon uptake in McLish Lake, 24 July 1962.

numbers of algae at the lower edge of the bloom. The distribution of *Oscillatoria* is very similar to the bacterial plates described by Kuznetsov (1958, 1959). The possibility of the metabolism of this community being supplemented by some other process than ordinary photosynthesis is strongly suggested.

The level of maximum C^{14} uptake is at 7 m where the light intensity is less than 1% (Figs. 7 and 8). This depth is much nearer the level of maximum phytoplankton density. The carbon uptake maximum at 7 m occurred both in the dark samples as well as in the samples representing only light reactions (C_p). In other words, it appears that a significant amount of the carbon absorbed at this depth is not resulting in the production of an equivalent amount of oxygen.

Oxygen production would not be expected from any kind of aphotic carbon uptake. Dark absorption of carbon ($C_t - C_p$ in Fig. 7 and C_d in Fig. 8) parallels very closely the population density curve of *Oscillatoria*. At 7 m, dark-absorbed carbon was equal to 38% and 47% of the light-absorbed carbon on two occasions (Eberly, 1964). In order to eliminate any possible effect of bacteria, a series of samples was filtered through a millipore filter of 5 μ pore diameter (MP type SM) and exposed in parallel with unfiltered samples according to the method of Kuznetsov (1958). Though the filtrate is presumed to contain chiefly bacteria, very small nannoplankton algae might have been present, so the biotic components are referred to collectively as microplankton. Total carbon uptake by the microplankton, including aphotic assimilation, appears to be negligible throughout the water column, even decreasing significantly in

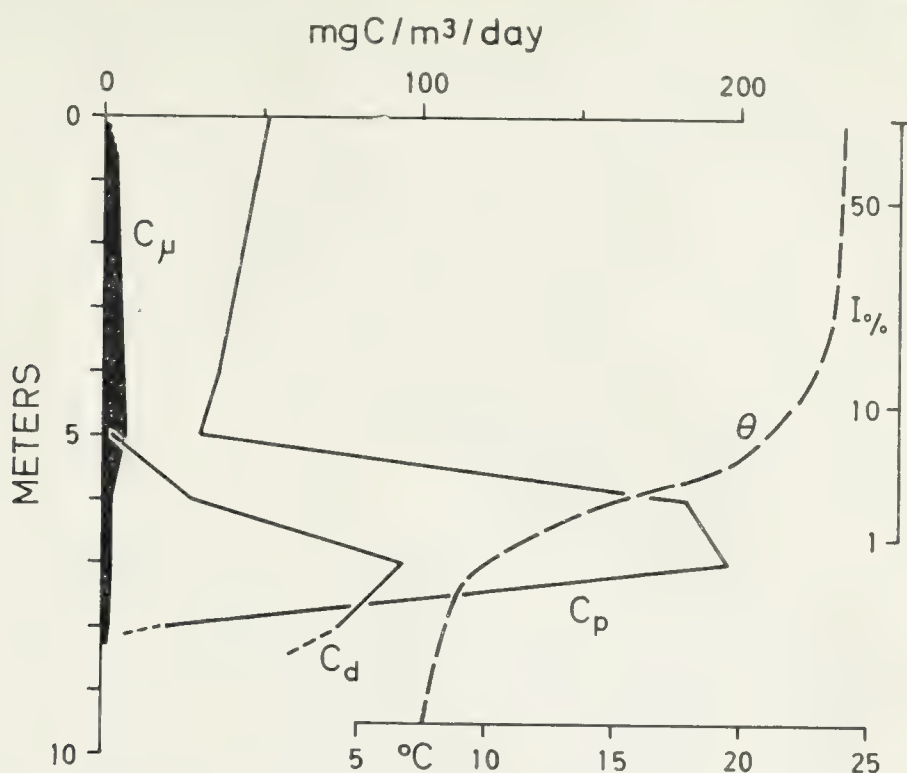


FIG. 8. Phototrophic (C_p) and aphotic (C_d) carbon uptake by algae ($>5\mu$) and total carbon uptake by microplankton (C_μ) in McLish Lake, 30 July 1962.

the metalimnion (C_μ in Fig. 8). Therefore both the curves C_d and C_p represent activity of algae alone (greater than 5μ in size). Microscopic examination reveals that this element of the plankton in the lower metalimnion consists almost entirely of *Oscillatoria agardhii*.

The great amount of aphotic carbon uptake (plus the imbalance that exists between phototrophic carbon assimilation and oxygen production) suggests that another energy source besides light is being used in the utilization of inorganic carbon. Whether anything similar to those chemosynthetic processes now understood for certain of the bacteria exists for *Oscillatoria* is not known. The only unusual chemical characteristic of the water of which the writer is aware is the presence of great amounts of sulfate (over 100 mg/L) and the presence of H_2S in the hypolimnion up to the lower surface of the plankton bloom. Nakamura (1938, as cited by Spruit, 1962) has described carbon dioxide assimilation in *Oscillatoria neglecta* and *Pinnularia* (?) with hydrogen sulfide as the hydrogen donor. Pringsheim (1963) has recently regarded *Oscillatoria* as being very close to *Beggiatoa*, which he considers to be a colorless blue-green algae both on morphological and physiological grounds. Forms identified as *Oscillatoria agardhii* have been reported from polluted waters, e.g., Fall Creek in Indianapolis (Chicago Natural History Museum, Cryptogamic Herbarium, courtesy Dr. Francis Drouet) and Norrviken (Sweden, courtesy Mr. Ingemar Ahlgren), a lake that receives the effluent from a yeast factory. Nearly colorless forms tentatively identified as *O. agardhii* var. *isothrix* have been found *en masse* in the polluted offshore waters near Stockholm (M. Waern and B. Lindahl, personal communica-

tion). Lakes rich in H_2S and dominated by *Oscillatoria* have been designated by Wundsch (1940) as " H_2S -*Oscillatoria*-Seen." In these lakes he finds mainly *Oscillatoria agardhii*, *O. redeckei*, and *Aphanizomenon gracile*. The very reduced turbulence in the hypolimnion of these lakes and the presence of H_2S below the plankton-oxygenated zone are very similar to Myers and McLish lakes, though the concentrations of H_2S apparently are not so great as in the European lakes.

All of these observations, though largely circumstantial, point toward the existence of a supplemental metabolic pathway in *Oscillatoria*, if not identical at least similar to that of the Beggiatoales. An alternative interpretation, that this aphotic carbon uptake represents assimilation without reduction resulting in the direct incorporation of carbon dioxide presumably in carboxyl groups, has been suggested by Fogg (1963). In any case it is perhaps appropriate to conclude with the final statement of Fogg in the paper just cited. "Before too much effort is expended on measurements of the productivity of lakes and seas it is essential that biochemists and ecologists should collaborate to find out exactly what these measurements represent." Certainly more knowledge is needed of the physiological ecology of *Oscillatoria agardhii* in order to understand more fully the development of the metalimnetic oxygen maximum.

DISCUSSION AND SUMMARY

Whenever the oxygen content of the metalimnion exceeds the vernal prestratification saturation value at 4° (12.7 mg/L at sea level), which is the maximum amount of oxygen that can develop through purely physical means, the metalimnetic oxygen maximum can be defined as a biogenic phenomenon. Such an oxygen maximum can occur only if the rate of oxygen production in the metalimnion exceeds the rate of oxygen loss through respiration and turbulent transfer. The *sine qua non* for oxygen production is the penetration of adequate light into the metalimnion. In lakes with an oxygen maximum approximately 10 to 50% of the light energy passes through the thermocline. The actual light intensity at the level of maximum oxygen production is generally much less than this, however, because oxygen maxima usually occur in the middle to lower strata of the metalimnion. Transparency is influenced by the intrinsic color of the water as well as the amount of suspended particulate matter, both allochthonous and autochthonous. A small watershed with good plant cover to reduce erosion is often associated with the more transparent lakes. Many glacial lakes are seepage lakes with no surface inlet.

Low plankton density in the epilimnion is the result of low nutrient levels. Nutrients may be limited by the nature of the drainage into the lake as well as by being consumed by the spring plankton blooms and subsequently trapped in the hypolimnion through sedimentation. The composition of the nutrient supply, both qualitative and quantitative, is a major factor in determining the species composition of the phytoplankton community as well as in affecting the rate of metabolism of the community. The specific nutrient requirements of many plankters, especially the Cyanophyta, are not known. Both diatom and bluegreen communities exist in the "normal" glacial lakes of Indiana and Wisconsin. When

suitable photic conditions exist in the metalimnion of some bluegreen lakes, *Oscillatoria agardhii* becomes dominant.

The "*Oscillatoria* lakes" of Wundsch (1940), though containing *O. agardhii* as well as *O. redekei* as dominant organisms, differ from the *Oscillatoria* lakes of Indiana. The German lakes are enriched with great amounts of organic matter, possess mild currents through the epilimnion although the hypolimnion is quite stable under pronounced thermal stratification, and develop the plankton bloom in the epilimnion. *O. agardhii* (including var. *isothrix*) occurs in many lakes in northern Europe, but is not known to be associated with oxygen maxima in the metalimnion. The oxygen maxima in the Alpine lakes is produced mainly by *O. rubescens*. Most of these lakes have an interesting and well-documented history of eutrophication since the beginning of the present century. Other than the enriched condition of the water, the general ecology of *O. rubescens* resembles that of *O. agardhii* in Myers and McLish lakes.

Some cause must exist to explain the presence of the dense *Oscillatoria* bloom at a specific level. Either the algae possess rather strict requirements of light and temperature and are able to "seek out" levels where such environmental conditions are optimal by varying the cell density through changes in the gas vacuole system, or the algae are concentrated at a particular level through some action external to the cells and subsequently develop into blooms if the conditions at this depth happen to be near optimal levels.

Within the metalimnion there is a plane of minimum turbulence (and maximum stability). The stability at this plane increases as the thermocline approaches the center of gravity. With some turbulence both above and below this plane, a more-or-less stagnant layer may develop which retains or traps plankton organisms. If conditions of light and temperature at this plane are within the limits of tolerance (though not necessarily optimal) for even one species, a stable population will develop. The more extreme the conditions of light and temperature, the fewer species can survive. Presumably *Oscillatoria agardhii* blooms under such conditions of low light intensity and temperature that no other species survives or at least develops competitive populations. Preliminary laboratory experiments with *O. agardhii* var. *isothrix* Skuja from Swedish waters indicate that massive growth can occur at higher temperatures and light intensities, suggesting that the conditions as they exist in the metalimnion of Myers and McLish lakes are in fact not optimal for this species. In other words, the bloom in nature develops in the absence of competition, not in response to optimal conditions in the metalimnion. Under laboratory conditions cultures contaminated with *Scenedesmus* or *Chlorella* are in a very short time completely dominated by the latter forms. An alternative hypothesis that *Oscillatoria* excretes an antibiotic or antialgal substance has yet to be tested.

Oxygen consumption through respiration in the metalimnion would be somewhat reduced because of the lower temperatures existing there. In Myers and McLish lakes no great population of zooplankton is associated with the *Oscillatoria* bloom, which would also reduce the respiratory demands of the community for oxygen. Perhaps this is related to the limited food value of *Oscillatoria*. The only zooplankter known to

the writer to use *Oscillatoria agardhii* as food is the ciliate *Nassula aurea*, which occurred in great numbers in the hypolimnion of Myers Lake in the summer of 1952, grazing on the lower boundary of the *Oscillatoria* bloom. If the algal species that could develop under the conditions existing in the "eddy trap" were desirable food organisms and appropriate herbivores were present among the zooplankton, it is doubtful that a phytoplankton bloom would develop.

Oxygen loss through non-biotic means occurs through molecular diffusion and mechanical transport by eddy currents. Molecular diffusion of oxygen is such a small value that it is generally safe to disregard it (Hutchinson, 1957). Transport by eddy currents can be a significant factor. However, it might also be said that turbulence sufficient to move much oxygen would also carry off the algae, thus preventing the development of a bloom. Conditions of stability and the absence of turbulence as they effect the concentration of algae at a specific level would have the same effect on oxygen accumulation. Such stability is influenced considerably by lake morphometry as well as various external factors such as climate and lake surroundings. Greatest stability in small lakes is reached when the maximum depth is at least 2% to 3% or more of the diameter (relative depth). Highest oxygen values in US lakes are associated with lakes with relative depths of about 4%. Because the wind initiates and enervates turbulence and currents in lakes, any physiographic feature that shields the lake from direct effect of the wind will induce a stagnation within the water mass independently of the thermal stability in the Schmidt sense. Such edaphic stability appears to be a major factor in the Alpine lakes where variations in morphometry do not seem to be related to variations in oxygen stratification. It is also important in small lakes surrounded by hills and trees (e.g., Otter Lake in Wisconsin). In this respect, the calculation of the actual amount of eddy diffusion within the lake (clinolimnetic coefficient of eddy conductivity) might be more significant than the stability of stratification.

The major points in the present paper may be summarized as follows:

1. The term "plus-heterograde" is most useful when describing oxygen profiles in which the metalimnetic oxygen maximum exceeds the vernal prestratification saturation value at 4° (12.7 mg/L at sea level), which represents the maximum amount of oxygen that can be present in the water through purely physical means.

2. A *plus-heterograde lake* is one that maintains a plus-heterograde oxygen profile throughout most of the period of summer stratification until the beginning of fall circulation.

3. Area and relative depth are the morphometric parameters that are most closely associated with the development of the metalimnetic oxygen maximum. In the US lakes, oxygen maxima are most likely to be found in lakes under 30 ha and with relative depths of about 4%. In mountain lakes morphometry is less important because of the edaphic stability resulting from the absence of pronounced wind disturbance.

4. Four types of oxygen maxima are noted. *Pseudo-metalimnetic oxygen maxima* form under high thermoclines in small, well protected lakes. These so-called "secondary thermoclines" are unstable, eventually disappearing and thus incorporating the highly productive "pseudo-

metalimnion" into the epilimnion. *Temporary sub-climax oxygen maxima* form in the deep metalimnia of very transparent lakes early in the summer. The disappearance of the oxygen maximum in mid-summer is apparently due to the depletion of the nutrient supply and the subsequent decline of the phytoplankton community. *Permanent climax oxygen maxima* persist throughout most of the summer until the beginning of fall circulation and usually reach the highest oxygen values in late summer. Two sub-types, *Diatom maxima* and *Oscillatoria maxima*, are based on the dominant alga species.

5. The best known *Oscillatoria* lakes (Myers and McLish) are dominated by *Oscillatoria agardhii*, which produces dense blooms and high oxygen concentrations at temperatures of 10-12° C and light intensities of 1-3% of surface intensity. Photosynthetic efficiency at the level of maximum oxygen production ranges from 0.8% to 1.7%. The possibility that the metabolism of this species is augmented by some light-independent process perhaps involving H₂S is suggested.

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